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SALINITY-LINKED RESTRICTIONS OF PHYTOPLANKTON STANDING CROPS IN HIGH-PHOSPHORUS ALBERTA SALINE LAKES

by

JUDITH CATHERINE EVANS

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A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE.

DEPARTMENT OF BIOLOGICAL SCIENCES

Edmonton, Alberta

FALL 1995

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FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled SALINITY-LINKED RESTRICTIONS OF PHYTOPLANKTON STANDING CROPS IN HIGH-PHOSPHORUS ALBERTA SALINE LAKES submitted by JUDITH CATHERINE EVANS in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE.

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Date: 18 Aug 1995

Abstract

Shallow, closed basin saline lakes found in semi-arid areas tend to be extremely sensitive to changes in precipitation/evaporation ratios. Historical climatic information for this region indicate that the area is becoming increasingly arid and this trend is expected to continue under current climate-change scenarios, leading to increases in lake salinity. Data were available on water chemistries and phytoplankton of six Alberta saline (> 1 g L^{-1} total dissolved solids) lakes from a 12 year arid period and used to evaluate potential chemical and biological effects of climate induced increases in brine conductivity. Major ion concentrations, relative proportions of major ions, chlorophyll *a* (Chl *a*) concentrations and the relative importance of different phytoplankton phyla were evaluated with respect to the increasing conductivity profiles of the lakes and with respect to the range of conductivities represented in the lake series. When data from the six lakes were combined, concentrations of sodium, potassium, magnesium, sulfate, chloride and alkalinity were positively correlated with conductivity and calcium was negatively correlated with conductivity. The relative proportions of sodium, sulfate and chloride increased significantly with brine conductivity (2.9 to 30.9 mS cm^{-1}), while the proportions of other ions decreased. The variability of these relationships in the individual lakes suggests that the brine compositions in some of the lakes are strongly influenced by local surface water and groundwater chemistry. Increases in conductivity were usually accompanied by decreases in Chl *a* concentration and a shift away from cyanophyte species in favor of chlorophytes, cryptophytes and chrysophytes. This change in the importance of these phytoplankton phyla, which occurs at relatively low salinities (approx. 3.5 mS cm^{-1}), acts to limit phytoplankton biomass in these phosphorus sufficient systems by restricting the growth of nitrogen-fixing species. Salinity-linked shortages of nutrients may account for these changes.

Eleven saline lakes (including the six climate-change study lakes) were examined over the 1994 growing season to determine what salinity-related factor or factors were responsible for controlling phytoplankton standing crops. Lakewater salinity ranged from slightly saline to hypersaline (conductivity 1.8 to 58.8 mS cm^{-1}). The study lakes were characterized by high total phosphorus (0.15 to 24.2 mg L^{-1}), total nitrogen (3.75 to 12.35 mg L^{-1}), total iron

(55 to 2800 μg L^{-1}) and dissolved organic carbon (40 to 195 mg L^{-1}), but for the most part had low dissolved inorganic nitrogen concentrations (usually < 100 μg L^{-1}). Chl *a* levels in all but the two least saline lakes were extremely low (< 20 μg L^{-1}), up to three orders of magnitude below that predicted by freshwater phosphorus-based models.

High alkaline phosphatase activities (APA) and rapid ^{32}P-othophosphate uptake indicated that the two least saline lakes were P-limited; these lakes had seston deficient in P, N, and protein. APA and ^{32}P-othophosphate uptake were below detection in the more saline lakes (conductivity > 3 mS cm^{-1}), indicating P-sufficiency; seston from these lakes was deficient in N but (in all but one case) lacked the nitrogen-fixing cyanophytes that could relieve nitrogen deficiencies. Phytoplankton in lakes with conductivity > 3 mS cm^{-1} largely had normal (> 1.2) protein:carbohydrate ratios and, based on nutrient bioassays, were not limited exclusively by inorganic N availability, nor by a combination of Mo and N. Fe-addition bioassays indicated that Fe was limiting in all of the P-sufficient lakes except one. Alkalinity manipulation bioassays indicated that bioavailability of the Fe already present, which was largely particulate, was severely restricted by lakewater alkalinity. The most saline lake appeared to be limited by one or more additional trace elements. Zooplankton biomass was greater than the phytoplankton biovolume in lakes with conductivity > 3 mS cm^{-1} indicating the potential for severe grazing pressure. Zooplankton gut pigment analyses indicated that phytoplankton were consumed.

Lakewater alkalinity, which increases with conductivity in these prairie lakes, appears to be the key factor limiting Fe bioavailability and restricting phytoplankton standing crops as lake salinities increase. Alkalinity-linked iron limitation accounts for the conductivity-related decreases in Chl *a* and nitrogen-fixing cyanophyte importance observed in the lower-salinity lakes.

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Chapter 1

1.1 General introduction

Saline lakes occur in the dry areas of every continent (Hammer 1986a) and are a common feature of the Northern Great Plains. In much of this vast, semi arid region, saline lakes represent the only natural surface water available (Last 1992) and as such are an important resource for regional biota, including man. Estimates of the total volume of saline lake water in the world (104,000 km^3) are comparable to the estimated total volume of all freshwater lakes (125,000 km^3, Hammer 1986a).

Saline lakes form in areas of endorheic (internal) drainage where lake evaporation exceeds precipitation. Water is retained in the basin and salts brought into the lake remain there and evapoconcentrate. The ionic composition of saline lake water depends on the composition of salts available within the drainage basin and the relative solubilities of minerals within the lake after evapoconcentration (Hammer 1986b); both factors contribute to the large variation in ionic composition that exists in saline lakes worldwide. Although most saline lakes tend to be dominated by sodium, magnesium and calcium are also important in many lakes (Hammer 1986, Last 1992) and considerable variability exists with regards to anion dominance (chloride, sulfate, carbonate and bicarbonate). Lakewater pH tends to be basic (up to pH 11, Hammer 1986a) due to the presence of dissolved carbonate minerals in lake inputs, however, saline lakes in areas where mineral inputs are largely airborne marine salts or dissolved sulfides are known be acidic (pH as low as 3, Williams 1984).

Because changes in the concentrations of salts in saline lake waters are largely driven by changes in precipitation and evaporation rates, these waters are sensitive indicators of climate change. Changes in the salinities of lakes of the northern Great Plains region were noted as early as the 1920 to 1944 period (Rawson and Moore 1944), more recent increases in the salinities of these lakes (Hammer 1990), and other lakes worldwide (Williams 1991 and 1993) are currently considered a possible indication of climate warming.

Saline lakes are also used to examine climate changes on a longer time scale. Changes in lake salinity over time alter both mineral sedimentology (Vance et al. 1993, Van Stempvoort et

al. 1993, Vance and Last 1994) and fossil species composition (Fritz et al. 1991, Hickman et al. 1993) in saline lakes of the Great Plains. The use of fossil phytoplankton and zooplankton as indicators of past lake salinity reflects the profound biological effects of lake salinity on lake biota. Because many of the species found in saline lakes are derived from freshwater species (Williams, 1981), biodiversity tends to decrease as lake salinity increases beyond the tolerances of individual species (Hammer et al. 1975, Hammer 1990, Williams 1991, Williams 1993). These salinity-driven changes in lake biota are most noticeable at lower salinities, as many of the species found in saline lakes with TDS > 10 g L^{-1} are able to tolerate a wide range of salinities (Hammer et al. 1983, Hammer 1986a).

The evolution of salt lake brines by evapoconcentration of "fresh" inputs results in a salinity continuum with no clear dividing line between fresh and saline waters either in terms of lake chemistry or lake biota (Beadle 1969) The criteria for the classification of lakes as either fresh or saline waters is still a subject of much debate. Although the 3 g L^{-1} lower limit of salinity defined by Williams (1964), is the most generally accepted lower limit for saline waters (Hammer 1986a), this dividing line was based on taste, rather than a relevant fundamental limit. Other authors have argued that salinity-linked biological effects are apparent at far lower salinities and have suggested 1 g L^{-1} (Rawson and Moore 1944, Beadle 1969, Fan 1981) as a suitable boundary. Hammer (1986a) noted that there were classifications systems that defined saline water on the basis of as little as 0.21 g L^{-1} or as much as 5 0.21 g L^{-1} total dissolved solids (TDS) and proposed that lakes with TDS < 0.5 g L^{-1} should be classified as freshwater, those with TDS > 3 g L^{-1} as saline and those having TDS between 0.5 and 3 g L^{-1} as subsaline.

The classification of lakes as saline or fresh based on TDS mass concentrations does not take into account the variability of saline lakewater ionic composition (Ziemann 1968). Two lakes with TDS = 3 g L^{-1} but with different ionic compositions (e.g. sodium chloride vs. sodium bicarbonate brines) will have different ionic strengths. Since biological effects, such as osmotic pressure, are based on ionic strength rather than TDS, lake water conductivity appears to be a better basis for lake classification than TDS, however any classification system based entirely on

physical measurements may encounter problems when comparing lakes with different basic chemistries.

Prepas and Trew (1983) classified Alberta lakes with TDS > 0.5 g L^{-1} as saline, based on the observation that chlorophyll *a* concentrations in these lakes were below those predicted by freshwater phosphorus-based models. In general, prairie saline lakes do not fit freshwater models in which phytoplankton standing crop is determined by total phosphorus concentrations, with nitrogen fixation making up any deficiencies in nitrogen. Water from lakes in Alberta (Prepas and Trew 1983, Bierhuizen and Prepas 1985, Campbell and Prepas 1986), Saskatchewan (Robarts et al. 1992, my reanalysis of data in Haynes and Hammer 1978) and Manitoba (calculated from data in Barica 1975) often has far lower Chl *a* concentration than predicted by freshwater models. Although many of these lakes are still eutrophic, especially at TDS < 3 g L^{-1} , Chl *a* concentrations are often very low at higher salinities, even though total phosphorus concentrations tend to increase proportionately with salinity.

Nitrogen, rather than phosphorus, appears to be the limiting nutrient in many saline systems (Howarth 1988). The importance of nitrogen in controlling phytoplankton growth increased with increasing salinity in a series of coastal ponds (Caraco et al. 1987). Low inorganic nitrogen concentrations are able to control phytoplankton standing crop only in the absence of nitrogen-fixing cyanophytes, which make up for inorganic nitrogen deficits by chemically reducing nitrogen gas. Some saline lakes have extensive blooms of nitrogen-fixing species (Hammer 1969, Hammer et al. 1983, Horne and Galat 1985, Wood and Talling 1988), while others do not (Marino et al. 1990). Marine estuaries are typically far less productive than expected from their phosphorus concentrations and usually lack the nitrogen-fixing cyanophytes typical of high-phosphorus freshwater lakes (Howarth et al. 1988). Two major exceptions are the Peel-Harvey estuary (Huber 1986) and the Baltic Sea (Lindahl and Wallstrom 1985), where nitrogen-fixing species are abundant in the phytoplankton. The paradoxical absence of nitrogen-fixing species in the phytoplankton of saline lakes and estuaries with high total phosphorus has been the subject of numerous investigations.

Low trace nutrient bioavailability has been proposed as one of the reasons for low numbers of nitrogen-fixing cyanophytes in marine systems. Molybdenum and iron are both required for the synthesis of nitrogenase, the enzyme responsible for nitrogen fixation. Molybdenum limitation (Castle Lake) and molybdenum-iron colimitation (Lake Tahoe) were shown to be factors controlling phytoplankton growth in two freshwater lakes (Goldman and Amezaga 1984). Even though concentrations of these trace nutrients tend to be substantially higher in saline systems, nutrient bioavailability may be low due to the chemical environment produced by salt water.

In oxic waters, molybdenum is present as the molybdate anion, a species that is structurally and chemically similar to sulfate. Sulfate inhibition of molybdenum uptake was documented in many organisms, including phytoplankton (Cole et al. 1986), and it was proposed that low uptake rates were the key factor limiting nitrogen-fixation in marine systems (Howarth and Cole 1985, Howarth 1988). Because sulfate to molybdate ratios are relatively constant in seawater, the relationship between sulfate, molybdate and the relative importance of nitrogen-fixing cyanophytes was examined in a series of 13 Alberta prairie lakes, which acted as partial chemical analogs of marine systems (Marino et al. 1990). In this study, sulfate to molybdate ratios in saline lake water were related to the relative proportion of nitrogen-fixing cyanophytes in the lake phytoplankton communities.

The goals of this research were twofold: (1) determination of the chemical factors responsible for limiting phytoplankton standing crop in a series of 11 Alberta saline lakes, including eight of the lakes examined by Marino et al. (1990) and (2) evaluation of salinity-linked changes in ion chemistry and phytoplankton observed in six of the lakes over a 12-year arid period. Prairie saline lakes are both abundant and highly variable in their water chemistries and as such offer great scope for examining the effects of salinity on nutrients and biota outside the confines of the laboratory.

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Chapter 2

Potential effects of climate change on ion chemistry and phytoplankton communities in prairie saline lakes. [1]

2.1: Introduction

Models based on the atmospheric accumulation of greenhouse gases predict a rapid global warming trend that, among other changes, is expected to lead to increased aridity in the continental interiors (Ramathan 1988). In recent years, increasing concern over the impacts that this climate shift may have on north-temperate lakes has led to the use of long-term climatic and limnological records as means for predicting the chemical and biological changes that may occur in a warmer, drier future. Saline lake paleoecology has been a valuable tool for determining past climate trends in both temperate (Fritz et al. 1991) and subarctic (Pienitz et al. 1992) North American lakes, while examination of mineral deposition processes in saline lakes and playas may also provide considerable information on past environmental and hydrological conditions (Last 1994). Sedimentary studies combining both biological and mineralogical techniques have been used to determine past salinity changes in Canadian prairie lakes (Hickman and Schweger 1993; Van Stempvoort et al. 1993) on a long term basis, however, these core-based studies lack the fine resolution needed to examine the short-term salinity changes which play an important role in the ecology of these lakes. Historical data on past lake salinities and species assemblages can provide high resolution information on the effects of short-term climate variation and may act to supplement paleological studies in their predictions for a warmer climate regime.

The shallow, closed-basin saline lakes of the northern Great Plains are especially sensitive to changes in precipitation and evaporation, more so than the freshwater lakes found in the same region (where regular flushing activity acts to moderate the effects of evapoconcentration). Increases in the salinities of Saskatchewan saline lakes during periods of drought were examined as early as the 1920-1941 period (Rawson and Moore 1944). Hammer

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[1] A version of this chapter has been accepted for publication. J. C. Evans and E. E. Prepas. Limnology and Oceanography.

(1990) explored the relationships between long term salinity changes, lake level and variation in the mean summer temperature and annual precipitation in eight saline (> 3 g L^{-1} salt) lakes in Saskatchewan and Alberta. A study comparing lake surface area variability in humid, semi-arid and arid regions of eastern Alberta found that lakes in the semi-arid regions are the most sensitive to changes in weather patterns (Campbell et al. 1994). Lake levels in semi arid regions are controlled more by precipitation / evaporation ratios than by groundwater flux (as is the case in arid regions).

Although precipitation and evaporation rates greatly influence lake salinities, the effects of local differences in surface and groundwater cannot be ignored when evaluating the factors that determine brine composition and concentration. Last (1992) discusses the importance of groundwater chemical composition, precipitation to evaporation ratio, and the position of the lake basin with respect to elevation and drainage basin in the determination of lake brine chemistry. Morphology and underlying soil and bedrock types were of lesser importance. Swanson et al. (1988) found that geologic setting (in glacial till or sandy outwash) and the position in relation to local and regional groundwater flow systems influenced both the relative concentrations of ions and the relationship between ionic concentrations and conductivity in North Dakota saline lakes. Thus, it may not be possible to predict the changes in ionic composition that will occur in a single lake based on information gathered from lakes in a vast area - the effects of local hydrology may mask trends that are due purely to increasing salinity.

Increases in the salinities of several saline lakes in the semi-arid region southeast of Edmonton provided an opportunity to examine the trends in brine composition, chlorophyll *a* (Chl *a*) concentrations and changes in the importance of key phytoplankton taxa that are associated with increases in lakewater conductivity. Earlier studies of the relationships between salinity and major ion chemistry in Canadian prairie lakes (Last 1992) and Ethiopian lakes (Wood and Talling 1988) combined data from saline systems that showed a wide range in ionic proportions as well as geographic location. The variation in groundwater and surface-water chemistry that can exist over such vast areas may mask changes in lakewater chemistry that result from climate-driven changes in salinity. Water chemistry - conductivity relationships were examined in a group of 72

"saline" pothole lakes in a small (25 km radius) area of southwestern Manitoba (Barica 1975), but this survey included only 6 lakes with salinities > 3g L^{-1} total dissolved solids. This heavy use of lakes at the lower end of the salinity gradient limits the use of this study in examining trends in saline lake chemistry at higher salinities.

Last (1992) observed relationships between lake salinity, ion concentration and relative ionic proportions in a study of 491 saline lakes distributed across the vast Canadian Great Plains region. We will test if these relationships accurately describe the chemical behavior of six Alberta lakes (that were not included in Last's study), located in the aspen parkland - prairie transition zone. At the same time, we will examine changes in lake phytoplankton community that are associated with the changes in lake salinity and use this information to evaluate potential biotic implications of climate change.

2.2: Methods

Description of the lakes — The six saline lakes, Birch, Peninsula, Fluevog, Whites, Wappa and Joseph, are located in aspen-prairie parkland to the southeast of Edmonton, Alberta (Fig. 2.1). The lakes were selected from a larger group studied in 1983 (Bierhuizen and Prepas 1985) and 1987 (Marino et al. 1990) based on their wide range of salinities both as a group (2900 to 17,500 μS in 1983, Bierhuizen and Prepas 1985) and as individual lakes. Changes in the salinities over time were such that the highest conductivity found in one lake tended to overlap the lowest conductivity found in the lake of next highest salinity. This resulted in a nearly continuous conductivity profile for the lakes when data for the 1982-1994 period are combined. A seventh lake, Camp Lake, was used as a control with respect to changes in lake Chl *a* concentrations and phytoplankton communities. Camp Lake is a slightly saline (conductivity approx. 1850 μS cm^{-1} in 1983 and 1987) that lies in the same general region as most of the study lakes. Although the average seasonal conductivity in Camp Lake fluctuated somewhat on a yearly basis, this conductivity remained relatively constant compared to the other lakes studied, possibly due to its slightly greater depth (4 m maximum) and the presence of a

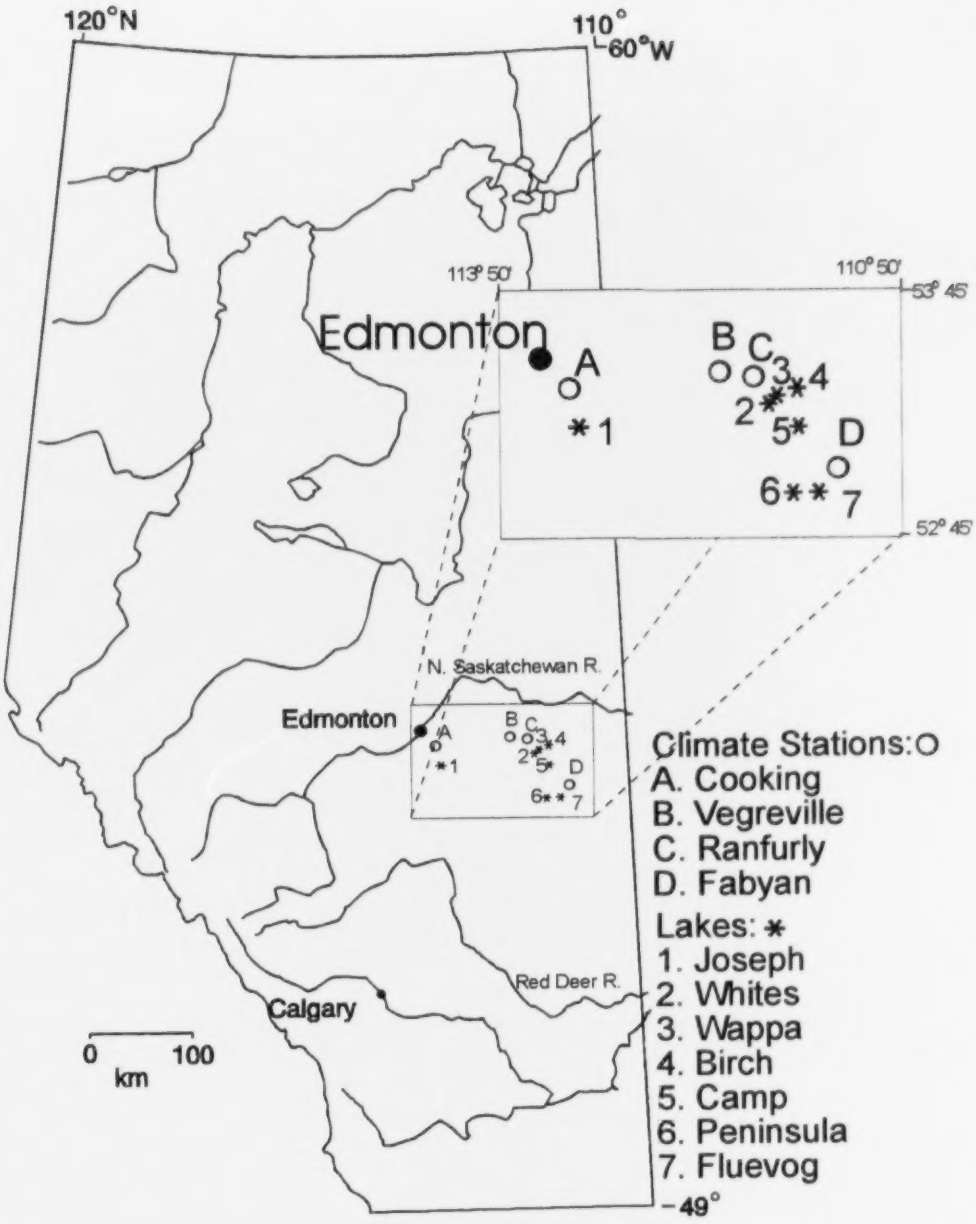

Fig. 2.1: The Province of Alberta: major rivers, locations of saline lakes (*) and Environment Canada Atmospheric Environment Monitoring Service monitoring stations (o) in the study area.

temporary outlet during rain events. All seven lakes are surrounded by agricultural lands, primarily grain and canola cultivation, with some ranching. The climate is continental, with mean annual precipitation and lake evaporation of 300-450 mm and 600-700 mm, respectively (Fisheries and Environment Canada 1978). The terrain varies from flat open plain to gently undulating hills, and the lakes are vulnerable to wind action.

The six study lakes are relatively small and shallow (surface areas 0.3 - 5.9 km^2, maximum depths 1.5 - 3.1 m). Most have large shallow areas and have no permanent surface inflows or outflows, thus the water balance and salinity are controlled by precipitation, evaporation and groundwater flux. All seven of the lakes had water present in the basins throughout the study period. In 1983, sulfate, bicarbonate and carbonate were the dominant anions, the dominant cation was sodium, pH ranged between 9.0 and 9.7, and phosphorus concentrations were high throughout the open water period (230 - 14,000 $\mu g\ L^{-1}$) (Bierhuizen and Prepas 1985). The lakes were not thermally stratified during the 1983 and 1987 summer study periods (Bierhuizen and Prepas 1985; Marino et al. 1990). Examination of orthophosphate uptake rates in water from Fluevog and Peninsula lakes in 1984 (Campbell and Prepas 1986), indicated that the lakes were not phosphorus limited. All of the lakes were fishless (Marino et al. 1990). Details of the physical, nutrient and biological characteristics of these lakes are given in studies from 1983 to 1987 (Bierhuizen and Prepas 1985; Campbell and Prepas 1986; Marino et al. 1990).

Field Collection — Although data for this study were collected from work done by several scientists over a 12-year period, field sampling was based out of a single laboratory, and methods were relatively consistent, allowing for year-to-year comparisons.

Joseph Lake was first sampled in 1981 (Prepas and Trew 1983); the other lakes were sampled once in the late summer of 1982 as part of an initial survey of the region's saline lakes. They were all sampled every three weeks from May through September 1983 (Bierhuizen and Prepas 1985) and, in addition, Fluevog and Peninsula lakes were sampled every two weeks from

April through September in 1983 and 1984 (Campbell and Prepas 1986). The lakes were then sampled monthly from May through August 1987 (Marino et al. 1990), and all except Birch L. were sampled again as part of a monitoring program in 1990, 1991 and 1992 (four, six and five times, respectively) from May through August of each year. Birch Lake was sampled five times in 1992. Joseph, Wappa, Whites, Birch and Camp lakes were sampled seven times from May through September 1994, Peninsula and Fluevog lakes were sampled once in early August 1994.

Details of the sampling techniques used in 1982-84 and 1987 may be found in Campbell and Prepas (1986) and Marino et al. (1990). Sampling in 1990, 1991 and 1992 followed the same protocol as for 1987. In 1994, the sampling technique was modified to reduce the risk of contamination from bottom sediment and sampling equipment according to the method described for molybdenum sampling in Marino et al. (1990), using opaque 2-L Nalgene bottles that had previously been acid washed in 50% nitric acid, rinsed five times with DDW and twice with lake water prior to filling. Water samples for ^{32}P-uptake and alkaline phosphatase activity analyses were kept at air temperature, samples for all other analyses were kept on ice.

Laboratory Analysis — Details of the analytical methods used from 1982 - 1987 are found in Bierhuizen and Prepas (1985), Campbell and Prepas (1986) and Marino et al. (1990). Methods used for 1990-1992 and 1994 samples were generally the same as those used in earlier studies - modifications are noted as follows. Dilutions were performed as needed to keep analyte concentrations within the linear ranges of the methods.

Conductivities in 1992 and 1994 were measured at 25°C. Measurements made prior to 1992 at 20°C were corrected to 25°C to allow year to year comparisons. Alkalinities were determined in 1994 by titration with a Mettler DL 21 Autotitrator equipped with a glass electrode and 0.5 N sulfuric acid. Values for alkalinity include all anions present that were titrated at pH > 4.3. Sample pH was determined at the same time as the alkalinity titration, which was performed within 24 h of sampling on water at 20°C. Sulfate and chloride were determined for 1994 samples by the ion exchange method used in 1987 (Marino et al. 1990). Relative anion

proportion was calculated by dividing the concentration of each anion, expressed as meq. L^{-1}, by the sum of the concentrations of sulfate, chloride and alkalinity.

In 1990, 1991, 1992, and 1994, samples for sodium, potassium, calcium and magnesium were filtered through acid washed, DDW rinsed, 0.45 μm HAWP Millipore membrane filters and acidified to pH< 2 with concentrated nitric acid within 24 h of sampling. Acidified samples were kept refrigerated at 4°C until analyzed in duplicate on a Perkin Elmer AA spectrophotometer (model 3030 from 1990 to 92, model 3300 in 1994). Sodium and potassium were analyzed by atomic emission, calcium and magnesium by atomic absorption using an air-acetylene flame (Environment Canada 1979; Ingle and Crouch 1988). Interference from carbonate was eliminated by the acidification of the sample. Calcium and magnesium were determined once in 1990. All four cations were measured five times in 1991, twice in 1992, and four times in 1994. Relative cation proportion was calculated by dividing the concentration of each cation, expressed as meq. L^{-1}, by the sum of all four major cation concentrations.

Total phosphorus (all years), total dissolved phosphorus (determined in all years except 1992) and soluble reactive phosphorus (1983-84 and 1994 only) were determined in duplicate by the methods described in Campbell and Prepas (1986).

Orthophosphate uptake rates were determined in Fluevog and Peninsula lakes five times over the June - August 1983 and April - August 1984 periods (Campbell and Prepas 1986). Uptake rates on Birch, Whites, Wappa, Joseph and Camp lakes were determined once in mid-July 1994. Experiments were run in duplicate in which 1 ml (185 KBq ml^{-1}) of carrier-free ^{32}P-orthophosphoric acid (DuPont) was added to 100 ml of lake water. The assay method of Lean and Rigler (1974) was modified; 25 mm fritted glass disc-filter holders were fitted with 0.22 μm GS Millipore membrane filters. At timed intervals, 1-ml aliquots of the treated lake water were filtered, and tower and filter were rinsed with untreated lakewater. The filters and seston were placed in glass scintillation vials, 10 ml of Fisher Scintisafe fluor was added and the samples were counted within 48 h on a Beckman LS 6500 Multipurpose Liquid Scintillation Counter. Experiments were started at lakeside within 30 min. of sampling and continued at lakeside and in

the laboratory for 5-10 h. Suspended detritus and clay particles present in water from many of the lakes caused the filters to clog rapidly and as a consequence, these experiments used smaller aliquots (1 vs 5 ml) and higher tracer concentrations (1850 vs 250 KBq L^{-1}) than those used in studies of less turbid systems in the same region (Campbell and Prepas 1986; Prepas 1983).

Alkaline phosphatase activity was measured four times from July to September 1994 by the method of Hill et al. (1968), as modified by Pick (1987). To compensate for the low phytoplankton levels found in most of the study lakes, we modified this method further by using 25 ml aliquots of lake water and adding the 3-o-methylfluorescien phosphate substrate at a final concentration of. 0.14 μM. Duplicate experiments were run within 24 h of sampling at 20°C rather than 35°C to more closely reproduce the conditions found in the lakes. Measurements were taken at time 0, 15, 30 and 60 min. Sterilized DDW served as a control. Since the lake water was sufficiently turbid so that significant quenching of the fluorescence occurred, the method was calibrated for each lake sampled with standard additions of 3-o-methylfluorescein. Analyses were performed in duplicate within 24 h of sampling on lake water that had been kept at 20°C.

Analysis of Chl *a* was determined for all samples by the method described in Bierhuizen and Prepas (1985) Filtration took place within 8 h of sampling, extraction and analysis of frozen filters was performed within three weeks. Lake phytoplankton composition was determined in 1987, 1991 and 1994. Samples for phytoplankton enumeration were preserved within 6 h of sampling with Lugol's iodide fixture and counted on an inverted microscope by the sedimentation technique of Lund et al. (1958). Biovolumes were calculated based on an average cell volume (using 10-20 cells) of each species observed. Cell volumes were based on cell geometry and were calculated for each sample. The biovolumes of larger diatoms and some of the colonial species (such as *Pediastrum duplex* Mayen) were determined on an individual basis. Phytoplankton were identified to species wherever possible (Findlay and Kling 1979; Whitford

and Schumacher 1984). Lugol's solution was added to the stored samples periodically, since the saline lake water slowly reduced the iodine to iodide.

Climatic information — All climate data were obtained from the Environment Canada Atmospheric Environment Service. Long-term annual mean daily minimum, maximum and average temperatures, as well as rainfall, snowfall and total precipitation data were obtained for the 1905 to 1992 period at the Ranfurly monitoring station (Fig. 2.1). Annual mean summer (May through August) temperatures were calculated from monthly temperature data for this same period. Annual total precipitation data were obtained, where available, for the 1982 to 1993 period at three monitoring stations (Ranfurly, Fabyan and Cooking) in the study region (Fig. 2.1). Lake pan evaporation data were obtained from the monitoring station in Vegreville.

2.3: Results and Discussion

Climate — Linear regressions of temperature and precipitation records from Ranfurly station (1905 to 1992) (Fig. 2.2) with time (1905 to 1992) indicate a decreasing trend ($\underline{P} = 0.025$) in annual total precipitation and an average increase of 0.0133 °C yr^{-1} ($\underline{P} = 0.006$) in annual mean daily temperature. This increase in annual mean daily temperature is largely driven by a ($\underline{P} < 0.0001$) trend in annual mean daily minimum temperature. Annual mean summer temperature (May through August) also increased ($\underline{P} = 0.003$). These long-term trends can be seen even against a background of considerable interannual variation and indicate that the region is slowly becoming more arid.

Within the shorter time scale examined by our study, changes in annual precipitation and evaporation can be linked to changes in lake salinity in subsequent years. Annual total precipitation data collected for the three climate stations show that, for a given year, considerable variation can exist within the region (Fig. 2.3). These local differences in precipitation may create differences in the patterns of salinity change in the various lakes. In addition, differences in the pattern of precipitation at the extreme local level may cause changes

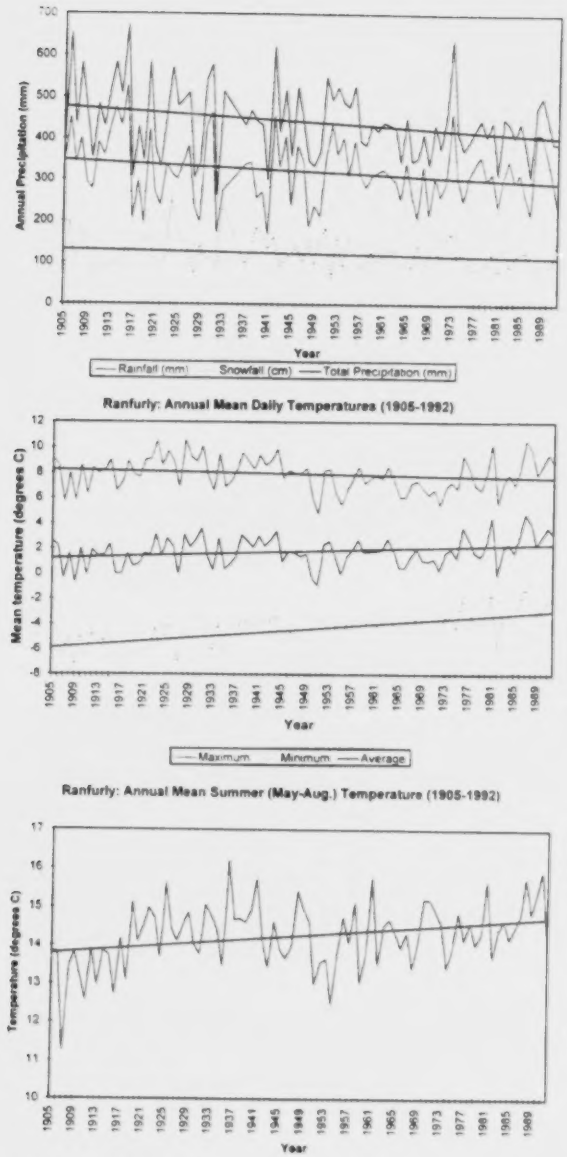

Fig. 2.2: Long term climatic trends for the saline lakes region. Data from Environment Canada Atmospheric Environment Service monitoring station at Ranfurly, Alberta. Linear regressions with time showing a decrease in annual precipitation ($\underline{r}$ = 0.24, $\underline{P}$ = 0.025) and increases in annual mean temperatures ($\underline{r}$ = 0.28, $\underline{P}$ = 0.006), annual mean daily minimum temperatures ($\underline{r}$ = 0.62, $\underline{P}$ << 0.001) and mean summer temperature ($\underline{r}$ = 0.32, $\underline{P}$ = 0.003) are significant ($\underline{P}$ < 0.05).

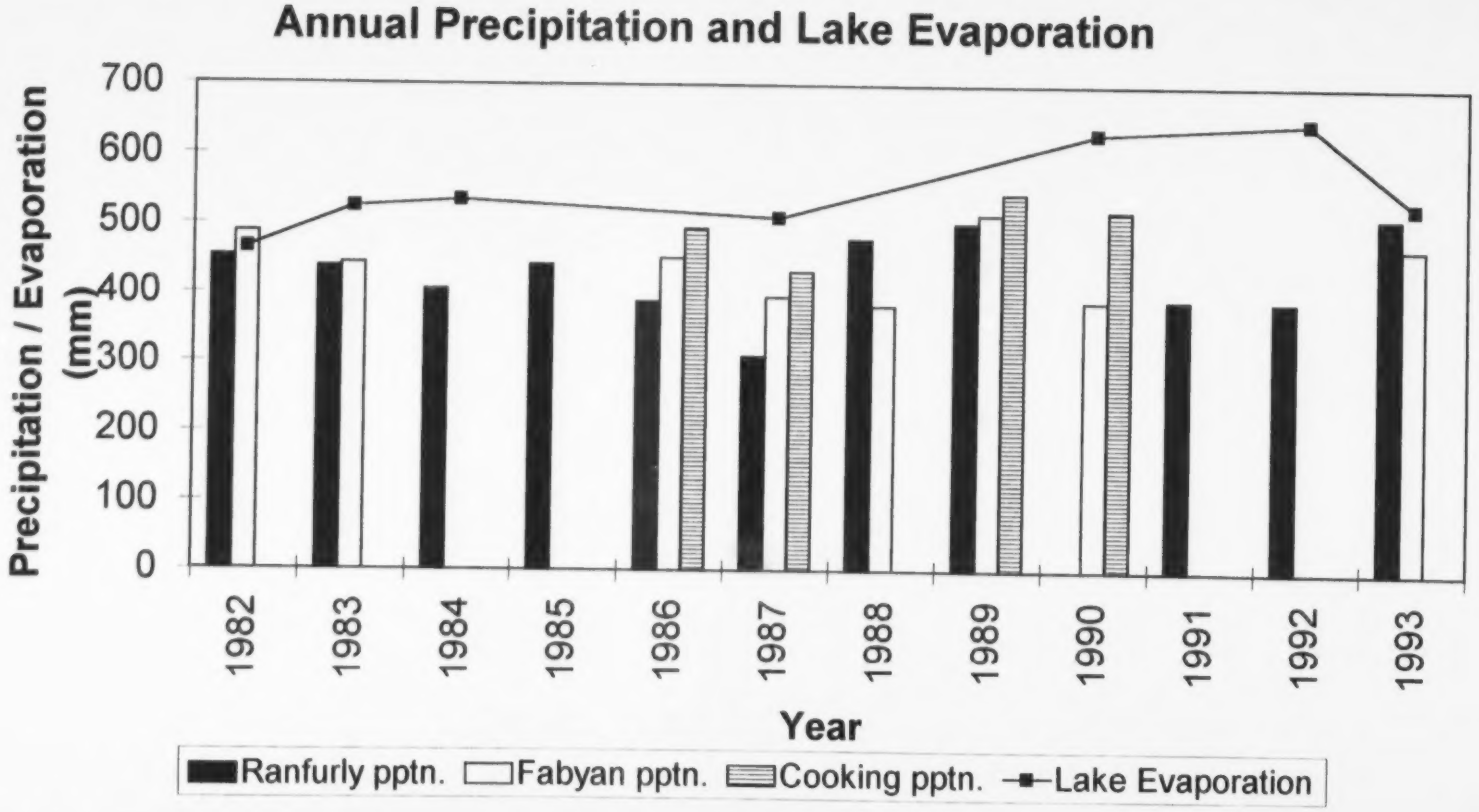

Figure 2.3: Annual summer (May through September) lake evaporation and available annual precipitation for weather stations in the saline lakes region during the study period. Data from Environment Canada Atmospheric Environment Service.

in lake salinity that cannot be explained by examination of station data. On several occasions during field sampling, we observed highly localized storms that drenched the area around one lake, while the ground a few km away remained dry.

Conductivity — In 1983, the conductivity of the water in our six study lakes ranged from 2900 to 17,500 $\mu S\ cm^{-1}$. Conductivity tended to increase in these lakes over the next 11 yr, coincident with increasing mean temperature, reaching to 3250 to 30,900 $\mu S\ cm^{-1}$ in 1994 (Fig. 2.8), although the pattern of conductivity change differs among the lakes. Differences in the 1990-1991 conductivity patterns of lakes (Whites, Wappa and Birch) that are only 5 to 10 km apart suggest that factors operating at an extremely local level may ultimately control a lake's salinity, although regional temperature and precipitation will also have a strong effect. In shallow, closed basin systems like the six study lakes, where the water balance is controlled by precipitation, evaporation and groundwater flux, decreased precipitation to evaporation (P/E) ratios will tend to give rise to lower water levels and, as a consequence, to increased lake salinities (Williams 1993). P/E ratios in the Ranfurly-Fabyan region were highest (0.97) in 1982 and 1993, and can be linked with the relatively stable lake salinities in 1982-83 and 1994. Lower P/E ratios (0.61) in 1987, 1990, and 1992 may be responsible for the large increases in lake salinity during the middle of the study period.

Ionic concentrations — The six study lakes were classified according to the relative abundances of the major cations and anions (Barica, 1975; Swanson et al., 1988) as having either mixed sodium sulfate-alkaline (Birch Lake) or intermediate sodium sulfate-alkaline (other five lakes) brine types. Since all of the study lakes have essentially the same basic water chemistry, trends in the concentrations and relative proportions of the major ions with increasing conductivity may be examined both for individual lakes and for the lakes as a group.

Sodium and potassium behave conservatively in individual lakes ($\underline{P} < 0.05$, Table 1), with some exceptions. In Fluevog Lake, potassium concentration was not correlated with conductivity

Table 2.1: Relationships between conductivity and ion concentrations and relative proportions in the six study lakes. All correlations are linear. Lakes are in order (from left to right) of increasing mean salinity.

Lake:	Joseph			Wappa			Whites			Fluevog			Peninsula			Birch		
Variable: Conductivity vs:	r	n	P	r	n	P	r	n	P	r	n	P	r	n	P	r	n	P
Sodium concentration	0.63	19	0.004	0.82	18	< 0.001	0.90	18	< 0.001	0.85	16	< 0.001	0.51	15	0.051	0.84	13	< 0.001
Potassium concentration	0.44	21	0.047	0.54	18	0.022	0.79	18	< 0.001	0.47	16	0.064	-0.01	15	0.918	0.84	13	< 0.001
Calcium concentration	-0.41	22	0.053	-0.59	20	< 0.001	-0.28	20	0.216	-0.66	17	0.005	-0.60	16	0.014	-0.51	14	0.06
Magnesium concentration	0.30	22	0.187	-0.41	19	0.08	0.39	20	0.092	0.26	17	0.289	-0.30	16	0.266	-0.01	14	0.842
Sodium proportion	0.35	19	0.148	0.79	17	< 0.001	0.52	18	0.028	0.62	16	0.011	0.67	15	0.006	0.47	13	0.107
Potassium proportion	-0.28	19	0.231	0.26	17	0.293	-0.58	18	0.012	-0.24	16	0.357	-0.39	15	0.159	0.01	13	0.962
Calcium proportion	-0.70	19	0.001	-0.79	17	< 0.001	-0.57	18	0.013	-0.71	16	0.002	-0.14	15	0.6	-0.63	13	0.021
Magnesium proportion	-0.30	22	0.187	-0.63	17	0.007	-0.28	18	0.268	-0.50	16	0.05	-0.57	15	0.024	-0.47	13	0.109
Sulfate concentration	0.79	14	0.001	0.95	14	< 0.001	0.94	14	< 0.001	0.98	11	< 0.001	0.10	9	0.844	0.97	13	< 0.001
Chloride concentration	0.74	14	0.002	0.85	13	< 0.001	0.94	14	< 0.001	0.84	11	0.001	0.77	10	0.009	0.95	14	< 0.001
Alkalinity concentration	0.42	28	0.024	0.71	27	< 0.001	0.71	28	< 0.001	0.79	34	< 0.001	0.46	37	0.004	0.72	21	< 0.001
Sulfate proportion	-0.40	13	0.172	-0.48	13	0.097	-0.66	13	0.013	0.57	11	0.07	-0.10	9	0.776	-0.01	12	0.929
Chloride proportion	-0.28	13	0.358	-0.10	13	0.775	-0.48	13	0.094	-0.58	11	0.061	0.44	9	0.241	-0.33	12	0.281
Alkalinity proportion	0.40	13	0.172	0.47	13	0.106	0.66	13	0.014	-0.52	11	0.102	0.10	9	0.835	0.01	12	0.882

($P = 0.064$), while in Peninsula Lake potassium concentration was not related to conductivity ($r = -0.01$) and the relationship between sodium concentration and conductivity was not significant ($P = 0.051$). When data from all six lakes was combined, the overall r values were 0.94 and 0.85 (Fig. 2.4), respectively, for sodium and potassium concentrations with conductivity. Overall, the trends in the concentrations of these monovalent ions are in agreement with patterns reported by Last (1992) in 491 "saline" (0.1 - 400 g L^{-1}) lakes in the Canadian Great Plains region and Barica (1975) in 72 Manitoba prairie pothole lakes (0.3 - 10 g L^{-1}).

Although Last (1992) found a positive correlation between calcium concentration and salinity for lakes across the Canadian Great Plains, we found a negative relationship. An inverse relationship is observed in all of the lakes and is significant in Wappa, Fluevog and Peninsula lakes ($P < 0.05$). The relationship between conductivity and magnesium is weak in the individual lakes ($r < 0.42$, $P > 0.08$), but there is an overall positive correlation ($r = 0.62$, $P < 0.0001$).

As predicted by Last (1992), the concentrations of the three major anions are all strongly correlated with conductivity in the combined lakes data (Fig. 2.5). Sulfate concentration and conductivity are positively correlated in five of the six lakes, while alkalinity and chloride concentration are correlated with conductivity in all of the lakes. The lack of a relationship between sulfate concentration and conductivity in Peninsula Lake water may be partly explained by missing data, since these ions were not measured during the 1990 to 1992 seasons when conductivity in this lake was highest. However, it is also possible that the variation in both sulfate and potassium is due to an influx of either groundwater or surface inputs containing unusually high or low proportions of these ions. The strong positive relationship ($r = 0.84$, $P < 0.0001$) between alkalinity and conductivity in our six study lakes accounts for the negative relationship between calcium concentration and conductivity. The concentration of calcium in many lakes is largely governed by the solubility of calcium carbonate minerals and in these high pH lakes, where a large proportion of the alkalinity is due to the presence of carbonate, it would be expected that calcium would precipitate as the alkalinity increased. This is the case in the Great Salt Lake, Utah, where the concentrations of calcium and carbonate do not increase with increasing salinity due to precipitation of calcium carbonate minerals (Eugster and Hardie 1978).

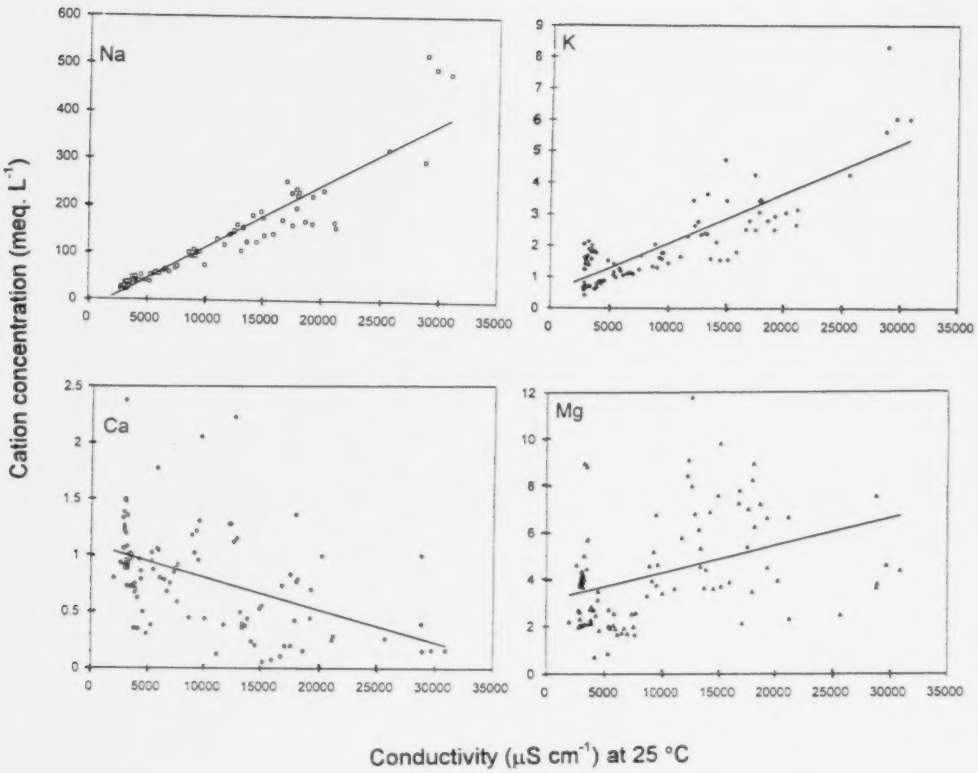

Fig. 2.4: Relationship between major cation concentrations (meq L-1) with conductivity for all six study lakes combined (1982 -1994). Each symbol represents one conductivity / cation measurement. Correlation coefficients for cations and conductivity are: sodium:0.94; potassium: 0.85; calcium: -0.68; magnesium: 0.62. All relationships are highly significant ($P < 0.0001$).

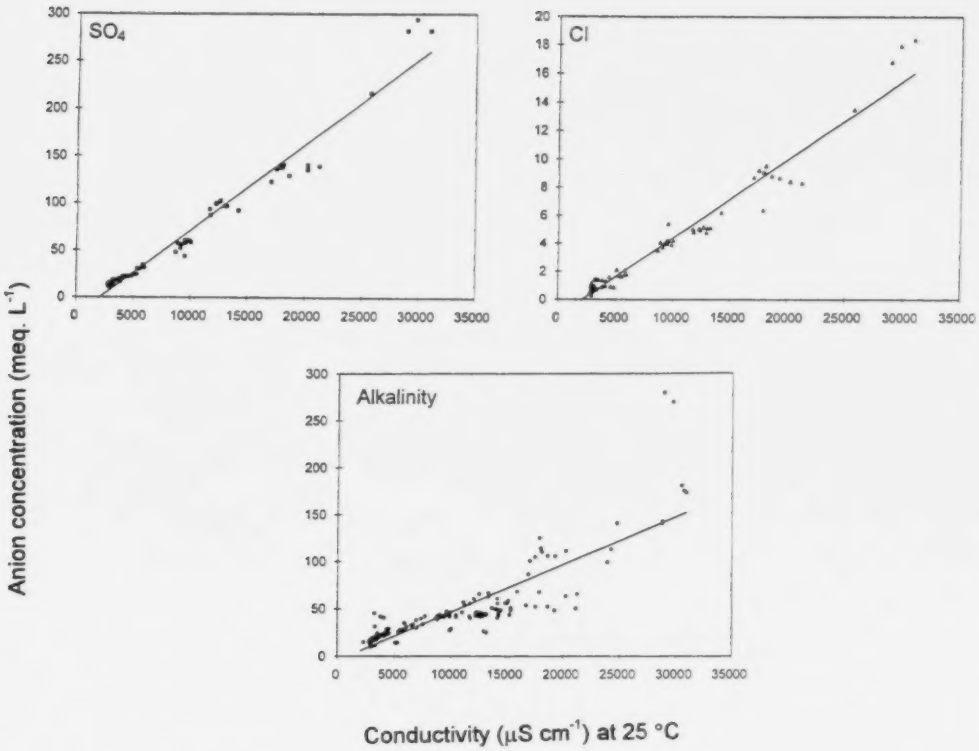

Fig. 2.5: Relationship between major anion concentrations (meq L-1) with conductivity for all six study lakes combined (1982 -1994). Each symbol represents one conductivity / anion measurement. Correlation coefficients for anions and conductivity are: sulfate: 0.98; chloride: 0.98; alkalinity: 0.84. All relationships are highly significant ($P < 0.0001$). (Alkalinity = bicarbonate + carbonate + hydroxide)

The relationship between the solubility of calcium and magnesium carbonates and the concentrations of calcium, magnesium and carbonate in high salinity systems is complicated by the effects of ionic strength. Ion pairing of calcium and magnesium with sulfate, bicarbonate and carbonate anions that acts to increase the overall solubility of these cations in saline waters (Bunce 1994). Interestingly, no correlation was found between calcium and carbonate concentrations in Last's (1992) study of 491 saline and subsaline lakes found on the northern Great Plains, probably because many of Last's study lakes were of low salinity (about half had TDS < 5g L^{-1}) and were not saturated with calcium carbonate. This stresses the need to examine trends in lake water chemistry at the local rather than the continental level.

Ionic proportions - Major cation proportions also have strong relationships with salinity in the combined lakes data (Fig. 2.6). Although they are largely independent of salinity at low conductivities, the proportions become salinity dependent above 4500 $\mu S\ cm^{-1}$. The best fit logarithmic / exponential regressions of cation proportions and conductivity are highly significant ($P < 0.0001$) for the combined lakes data set. This relationship is positive for sodium and negative for the other cations. In individual lakes (Table 1), the proportion of sodium is correlated with water conductivity in all but the least saline and most saline of the lakes; lakewater conductivity and potassium proportion are correlated only in Whites Lake. The proportion of magnesium is correlated with water conductivity in Wappa, Fluevog and Peninsula lakes, and that of calcium is correlated in five of the six lakes. Last (1992) found no relationship between lake conductivity and the proportions of sodium, potassium and magnesium, but the negative correlation between salinity and the proportion of calcium is in agreement with our findings.

Relationships between lake conductivity and the relative proportions of the major anions are weaker than that of the cations (Fig. 2.7). Although the proportions of sulfate and chloride had highly significant positive relationships with conductivity in the combined lakes data and the relative proportion due to alkalinity has a highly significant negative correlation, the situation in individual lakes is highly variable. As was the case for the cations, the relative proportions of

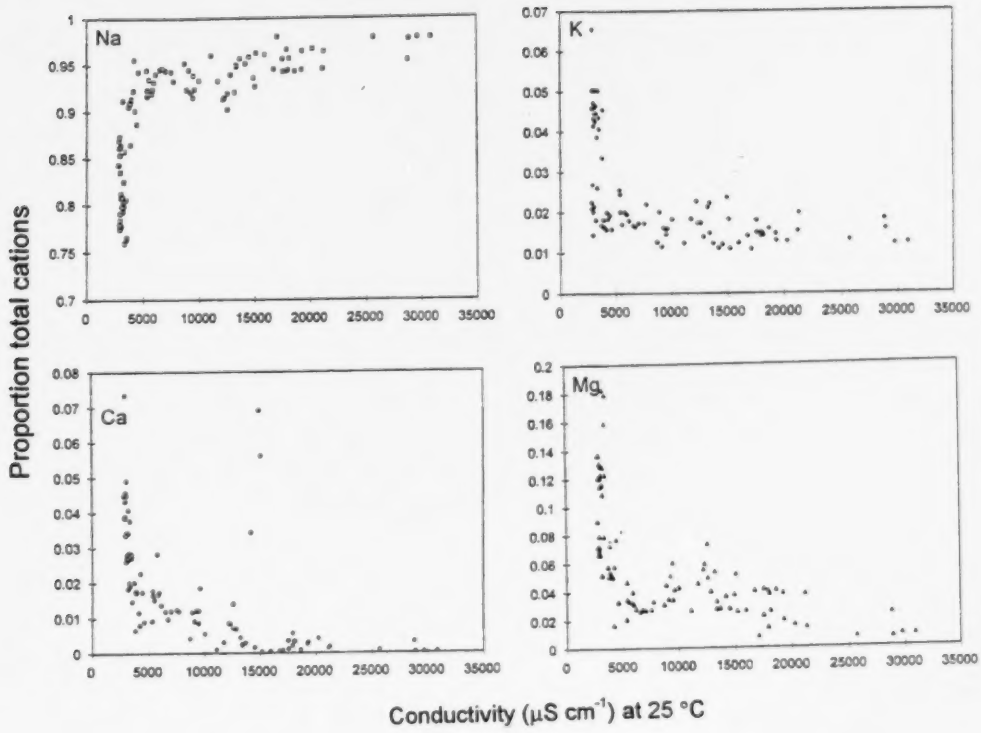

Fig. 2.6: Relationship between major cation proportions and conductivity for all six study lakes combined (1982 -1994). Each symbol represents one conductivity / cation measurement. Correlation coefficients for proportion of total cations and conductivity (from best fit exponential or logarithmic regression curves) are: sodium: 0.79; potassium: -0.71, calcium: -0.81; magnesium: -0.76. All relationships are highly significant ($\underline{P} < 0.0001$).

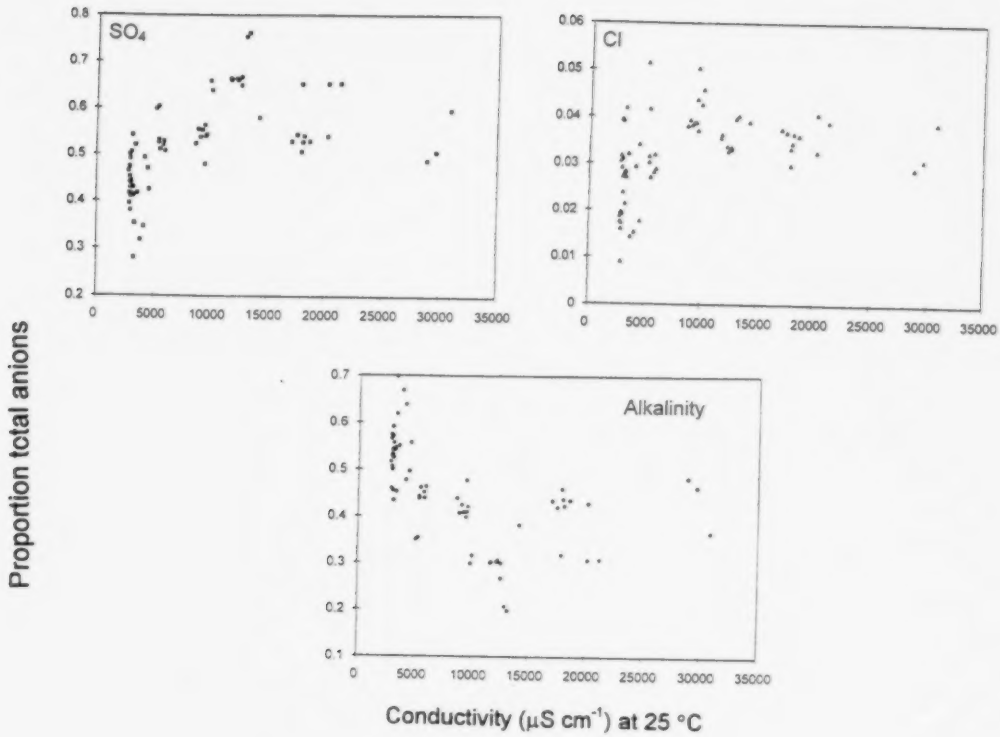

Fig. 2.7: Relationship between major anion proportions and conductivity for all six study lakes combined (1982 -1994). Each symbol represents one conductivity / anion measurement. Correlation coefficients for proportion of total anions and conductivity (from best fit exponential or logarithmic regression curves) are: sulfate; 0.66; chloride: 0.50; alkalinity: -0.63. All relationships are highly significant ($P < 0.0001$). (Alkalinity = bicarbonate + carbonate + hydroxide)

anions are largely independent of salinity at conductivities below 4500 $\mu S\ cm^{-1}$. In individual lakes, the only significant relationship between anion proportions and conductivity occurs in Whites Lake, where sulfate and alkalinity are, respectively, negatively and positively correlated with conductivity. In the non-significant relationships with $r > 0.50$, sulfate and chloride were negatively associated with conductivity, and alkalinity was positively and negatively associated, respectively, in Whites and Fluevog lakes. This indicates that the factors responsible for controlling the relative proportions of anions vary greatly from lake-to-lake, and predictions based on combined lake data cannot be used to predict anion proportions of individual lakes.

The change from salinity independent to salinity dependent ionic proportions at conductivities of approx. 4500 $\mu S\ cm^{-1}$ is of special note because this conductivity corresponds roughly with a salinity of 3 $g\ L^{-1}$ (Bierhuizen and Prepas 1985) in these lakes, the generally accepted lower limit of salinity proposed by Williams (1964). While this boundary was originally set by a somewhat arbitrary method (detection of brackish taste), our results suggest that lakes above and below 3 $g\ L^{-1}$ differ greatly with respect to the relationships between relative ion proportions and conductivity and that mineral saturation becomes important in these highly alkaline systems at relatively low salinities.

Phosphorus — The concentrations and bioavailabilities of phosphorus in the six lakes were examined to determine if the phytoplankton communities in any or all of the study lakes were phosphorus limited. In previous studies of the lakes of this region the relationship between spring total phosphorus and summer Chl *a* was positively correlated in freshwater lakes (Prepas and Trew 1983), but these parameters were not related in saline lakes (Bierhuizen and Prepas 1985). In a similar manner, total phosphorus (TP) was positively correlated with the relative biomass of cyanobacteria in freshwater Alberta lakes (Trimbee and Prepas 1987), but negatively correlated in saline lakes (Marino et al.). TP concentrations were high in all six lakes throughout the open water period, ranging from 230 to 14,000 $\mu g\ l^{-1}$ in 1983 and 1400 to 26,000 $\mu g\ l^{-1}$ in 1994. TP increased directly with conductivity in Joseph, Wappa, Whites and Birch lakes, a

relationship which is found commonly in freshwater systems, where decreased flushing rates during dry periods lead to increased concentrations of nutrients in the lake water (Dillon 1975). There was no relationship between phosphorus concentration and conductivity in Peninsula Lake, which also showed no relationship between lake water conductivity and two normally conservative ions, potassium and sulfate, suggesting that groundwater, rather than evapoconcentration, controls the salinity in this system. The negative correlation (r = -0.63, P) between TP and conductivity in Fluevog suggests that increases in lake salinity are leading somehow to increased losses of phosphorus, possibly through sedimentation.

In 1994, most (> 75%) of the TP in the six study lakes was present as soluble reactive phosphorus (SRP), a parameter not measured for most lakes in earlier years of the study. To ensure that the high SRP concentrations measured were not the result of acid hydrolysis of an unavailable phosphorus fraction during the analysis, alkaline phosphatase activity and orthophosphate uptake were measured in the lakes. Orthophosphate uptake experiments in water samples from Fluevog and Peninsula lakes in 1983 and 1984 found that their phosphorus turnover times were so long that they could not be measured experimentally (Campbell and Prepas 1986). In 1994, similar experiments in Joseph, Wappa, Whites and Birch lakes gave the same results. No significant ^{32}P uptake was found in any of the study lakes. The rapid uptake of the tracer in samples from Camp Lake, the control lake, indicated that the ^{32}P-orthophosphoric acid used was present in a readily available form. The results of the alkaline phosphatase activity analysis confirmed that phosphorus was readily available in the study lakes. No enzyme activity was found in the study lakes, but activities in water from Camp Lake exceeded 4000 nmoles methylfluorescein phosphate (μg Chl *a* hr)$^{-1}$, indicating extreme phosphorus limitation.

The high phosphorus concentrations found in the study lakes contrasted markedly with those found in phosphorus-limited Saskatchewan lakes of similar salinity (Robarts et al. 1992; Waiser and Robarts 1995) and allowed us to examine the changes in lake Chl *a* concentrations and phytoplankton communities with respect to conductivity without having to consider the effects of salinity-related changes to phosphorus availability.

Phytoplankton — Increases in lake conductivity at the lower end of the salinity gradient were generally accompanied by decreases in the frequency and magnitude of phytoplankton blooms (as measured by Chl *a* concentration) on a year-to year basis, although this relationship is poorly defined within a given growing season. This shift is especially noticeable in Joseph Lake (Fig. 2.8), where a rapid increase in conductivity in 1991 was associated with a sharp decrease in the magnitude of the summer Chl *a* peaks. An additional conductivity increase in 1994 coincided with a further reduction in summer Chl *a*. Although the spring phytoplankton community (Fig. 2.9) was mostly consisted of diatoms (primarily *Surirella ovata* Kuetzing) in all three years examined (1987, 1991 and 1994), summer phytoplankton changed from *Pediastrum duplex, Cosmarium* sp. Corda, *Closterium* sp. Nitzsch and *Crucigenia quadrata* Morren (Chlorophyta) in 1987, to the nitrogen-fixing cyanophyte *Aphanizomenon flos-aquae* Ralfs in 1991, and in 1994 to *Cryptomonas* sp. Ehrenberg in June, early July and September, *Botryococcus braunii* Kutzing in late July and *Aphanizomenon flos-aquae* in early August. Since the concentration of phosphorus in these lakes tends to increase with increasing conductivity, it would be expected that nitrogen-fixing cyanophytes would become more important as conductivity increased from 1991 to 1994, rather than the reverse as noted here.

A slightly different pattern was observed for Wappa Lake. Although increases in conductivity during the 1991 to 1994 period were generally accompanied by the expected decreases in Chl *a* concentrations, the period of lowest conductivity (1990) also coincided with low Chl *a* values. This phenomenon may be related to the phytoplankton bloom that occurred in mid-July 1987. This bloom of *A. flos-aquae*, with a Chl *a* concentration more than four times as high as any observed in the lake on any other occasion, may have altered the availability of trace nutrients in the water column in the following years. In 1991, the summer phytoplankton community was still dominated by *A. flos-aquae*, but the major species in early June was *Rhodomonas minuta* Skuja (Cryptophyta). In 1994, the summer phytoplankton community was composed of, at various times, *R. minuta, Microcystis aeruginosa* Kutzing (Cyanophyta) and

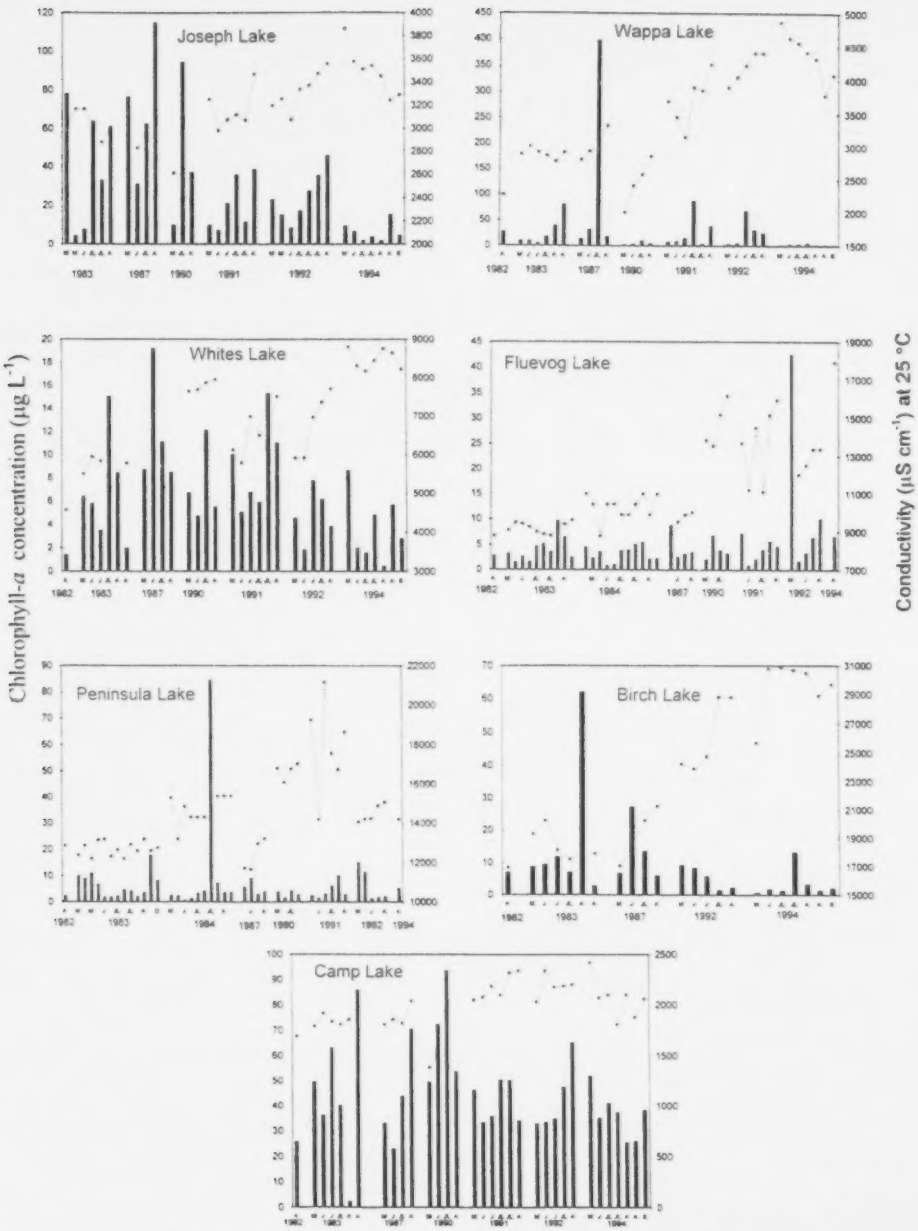

Fig. 2.8: Chlorophyll-*a* concentrations and conductivities (µS cm^{-1}) showing seasonal and year to year variation in the six study lakes (shown in order of increasing mean conductivity) and the control lake. Solid bars indicate chlorophyll-*a* concentrations, lines indicate conductivity. M = May, J = June, JL = July, A = August, S = September and O = October sampling dates.

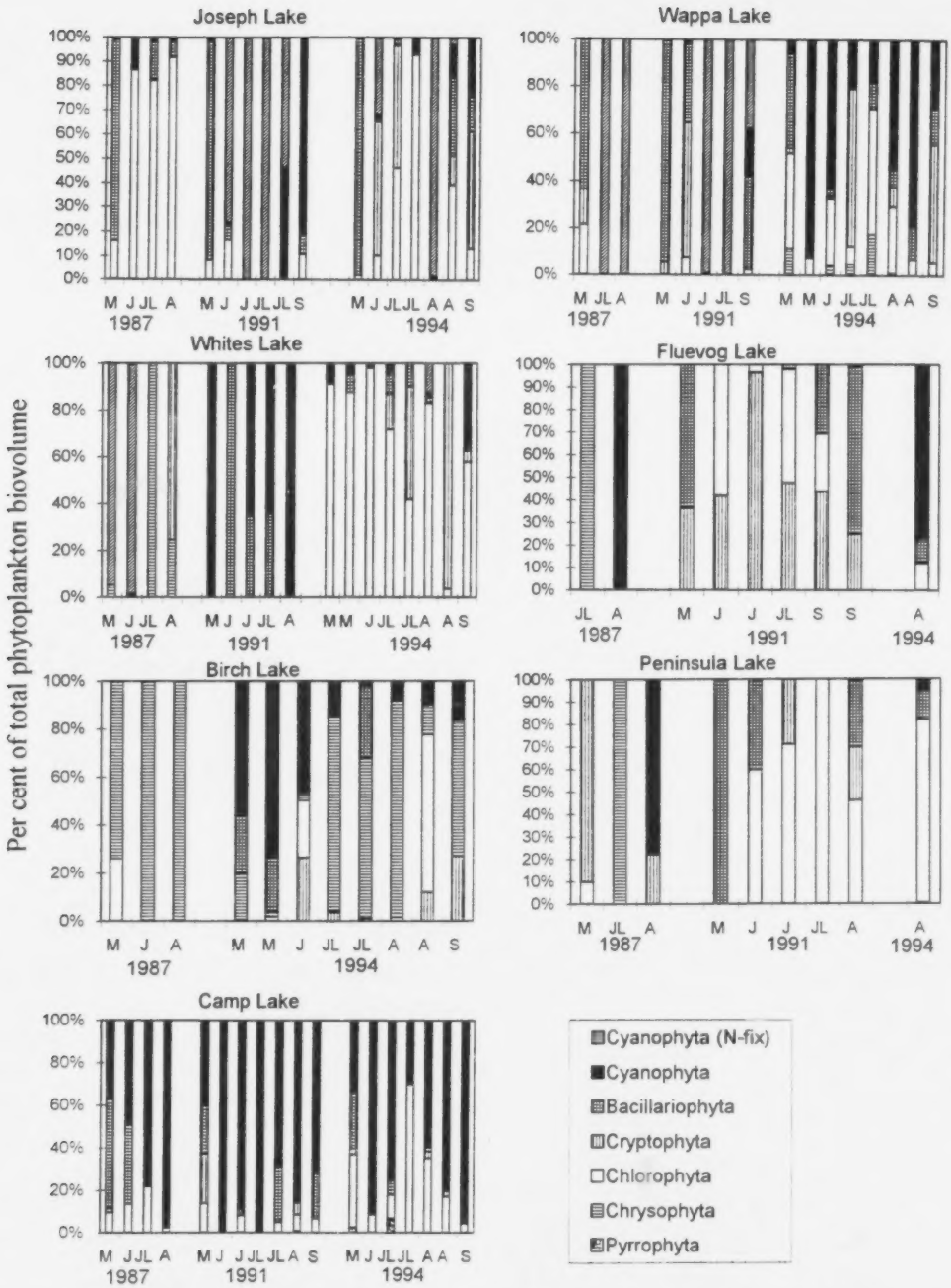

Fig. 2.9: Relative phytoplankton phyla abundances in the six study lakes (shown in order of increasing mean conductivity) and the control lake. M = May, J = June, JL = July, A = August, S = September and O = October sampling dates.

Oocystis borgei Snow (Chlorophyta). Spring phytoplankton in all three years were diatoms, primarily *S. ovata.* and *Cyclotella spp.* Kutzing.

Chl *a* concentrations tended to decline in Whites Lake as lake conductivity increased. In 1987, when lakewater conductivity was at its lowest (4000 to 5000 $\mu S\ cm^{-1}$), the spring phytoplankton was primarily *A. flos-aquae*, a species not normally noted for its presence early in the season. By mid-July, the most common phytoplankton species was *Chrysochromulina parva* Lackey, which was replaced by other chrysophytes and *R. minuta* in August. The 1991 spring phytoplankton again consisted of a typical "summer" species. *M. aeruginosa* was the most common species in the lake over the entire season, except in early June, when *S. ovata* was numerous. The shallow lake basin, which allows rapid warming of the lake water, may be a factor in the early appearance of species more often found (in freshwater systems) during the summer. In 1994, lakewater conductivity reached 8000 $\mu S\ cm^{-1}$, and the phytoplankton found was largely *O. borgei and C. quadrata* in the spring, early summer, and fall, and *R. minuta* in mid-August.

Fluevog and Peninsula lakes each had a phytoplankton bloom once during the period studied. The timing of the blooms; Peninsula Lake in July 1984 and Fluevog Lake in May 1992, does not appear to have any relationship to changes in the lakewater conductivity. Since phytoplankton species composition was not determined for either of these years, the identity of the bloom species is unknown, and it is possible that it was dislodged periphyton. Fluevog Lake phytoplankton consisted mostly of chrysophyte cysts and an unknown species of cyanophyte (non nitrogen-fixing) in 1987, *R. minuta, Ankyra judayi* Fott (Chlorophyta) and an unidentified diatom during 1991, and by *Chroococcus spp.* Nageli and *Oscillatoria* sp. Vaucher during August 1994. The most important species in Peninsula Lake was *R. minuta* in May and August 1987 and an unknown chrysophyte in July. In 1991, *Navicula sp.* Bory (Bacillarophyta) was replaced by *Surirella sp.* and *Characium sp.* A. Braun (Chlorophyta) in early June, then by *O. borgei* and *R. minuta* in late June. *B. braunii* and *O. borgei* were common for the rest of the season. The August 1994 community consisted mostly of *O. borgei.* The conductivity of Fluevog and

Peninsula lake water fluctuated a great deal in 1991 (Fig. 2.8), and changes in the phytoplankton community during this year may reflect this instability.

Birch Lake phytoplankton bloomed once during the study period. This peak occurred in August 1983, when the conductivity of the lake water was at a low point (18,000 $\mu S\ cm^{-1}$). Increases in conductivity were largely accompanied by decreases in Chl *a* concentration, with the exception of a slight Chl *a* peak in July 1994 at a time when the lakewater conductivity was high (30,500 $\mu S\ cm^{-1}$). The only phytoplankton cells found in 1987 were chrysophyte cysts. The 1994 phytoplankton community was composed of nannoplankton (non nitrogen-fixing Cyanophyta) in May and June and chrysophyte cysts and *Oocystis borgei* over the rest of the season.

The conductivity of Camp Lake water remained relatively stable during the period of study although there was some noticeable year-to-year and seasonal variation. Chl *a* concentrations remained high throughout the study period, in some years showing great seasonal fluctuations (1983 and 1987) and in other years remaining relatively constant for an entire season. The species composition varied from year to year, but filamentous cyanophytes (non nitrogen-fixing) remained the dominant group, contrasting with the changing importance of various phytoplankton phyla in those lakes where extensive changes in water conductivity were observed.

The reasons for these changes in the phytoplankton communities are currently unknown. Perhaps the most critical change occurs at the low end of the salinity gradient (< 3000 $\mu S\ cm^{-1}$), where a slight increase in conductivity appears to severely restrict the growth of the nitrogen-fixing species *Aphanizomenon flos-aquae*. This restriction is not simply due to low salinity tolerance; *A. flos-aquae* has been reported in Saskatchewan saline lakes with salinities > 20 $g\ L^{-1}$ (Hammer, 1986), far greater than the salinity at which it vanished from Wappa Lake. Other cyanophytes appear to be vulnerable as well. *Microcystis aeruginosa* declined drastically in Whites Lake after the conductivity of the lake water rose from 7500 to 8500 $\mu S\ cm^{-1}$. This species has been reported in lakes with TDS > 50 $g\ L^{-1}$ (Hammer, 1986), so its decline also cannot be explained by low salinity tolerance. Salinity also does not explain all of the differences

in Chl *a* concentrations among the lakes. Birch Lake, the most saline of the study lakes, had a 1994 peak Chl *a* concentration greater than that of Whites Lake. Williams (1993) noted that increasing salinity had the greatest effect on saline lake fauna at moderate salinities (0.3 - 10 g L^{-1}). In these systems, the greatest changes in lake phytoplankton occur in the lakes of least salinity, either due to some direct effect of salinity or as a consequence of salinity-induced changes in the numbers and species of grazing zooplankton. While the less saline lakes tend to bloom more often and for longer periods of time than the more saline lakes, it is still not known what triggers a phytoplankton bloom in the more saline systems, although a sudden increase in the availability of a limiting trace nutrient is one possibility. Decreases in the availability of trace nutrients with increasing salinity is also one possible explanation for the low Chl *a* concentrations of these high phosphorus systems. If changes in trace-nutrient availability are linked to the high concentrations of sulfate (competition with molybdate, Marino et al. 1990) or carbonate (precipitation of metal hydroxides and carbonates) typical of lakes in the study region but not found in all saline lakes, the differences in Chl *a* concentrations found in these lakes and in the highly productive saline lakes found in other regions (Hammer 1981) may be explained.

Our results indicate that increases in closed-basin lake conductivities predicted under current climate change scenarios will have a significant impact on both regional water chemistry and the relative importance of phytoplankton phyla in saline lakes. Increases in conductivity will lead to increased brine concentrations of sodium, potassium, magnesium, sulfate, chloride and alkaline anions, decreased concentrations of calcium, and an increased dominance of the brine by sodium. Our results contradict some of the findings made by Last (1992) in a study of 491 saline lakes distributed across the entire Canadian Great Plains region and indicate that trends in lake chemistries should be examined on a local scale wherever possible, to separate the effects of increased salinity from the effects of local soil and groundwater chemistries. Even within the relatively small region examined, there are differences in chemistry trends which must be attributed to local differences in the chemical composition of surface water or groundwater. The results also indicate that conductivity may be a major factor in controlling phytoplankton bloom

frequency and magnitude and the distribution of key taxonomic groups, most notably nitrogen-fixing cyanophytes, in these phosphorus-rich lakes. There was no overall trend between conductivity and maximum Chl *a* concentration, but there is a tendency for an increase in conductivity to be accompanied by a decrease in Chl *a*. There are a number of possible explanations for this phenomenon, which is not observed in all saline ecosystems. Firstly, nitrogen-fixing species may simply have low salt tolerance, and there is insufficient inorganic nitrogen present to support a large biomass of any other phytoplankton group. This hypothesis was rejected because nitrogen-fixing cyanophytes exist at far greater salinities than those of the lakes of this study (Hammer 1986). Secondly, increases in conductivity also may act to increase the concentration of a substance toxic to phytoplankton. This is a possible explanation for the low phytoplankton levels, but it cannot explain the existence of occasional algal blooms in the lakes. Thirdly, increases in the concentrations of one or more ions may act to decrease the availability of a vital nutrient, either by direct interaction with the nutrient (precipitation, complexation or ion pairing) or indirect action (i.e.: competing for the same enzyme active sites). Because the study lakes are not phosphorus limited, factors controlling Chl *a* concentrations and the relative importance of phytoplankton phyla could be examined without having to consider changes in phosphorus availability that normally accompany changes in salinity.

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Chapter 3

Relative importance of iron and molybdenum in restricting phytoplankton growth in high phosphorus saline lakes.[1]

3.1 Introduction

Phosphorus has traditionally been regarded as the nutrient limiting phytoplankton biomass and productivity in aquatic systems (Schindler 1977). The relationship between phosphorus (P) and phytoplankton biomass and productivity has been documented in many studies of freshwater systems (Dillon and Rigler 1974, Smith 1979). In these lakes, nitrogen fixation (N_2 fixation) by planktonic cyanophytes is able to make up for any existing deficiencies in nitrogen (N), leaving P as the limiting nutrient (Schindler 1977, Flett et al. 1980, Howarth 1988). In saline systems the relationship between P and phytoplankton standing crop is not as robust. Phytoplankton chlorophyll *a* (Chl *a*) concentration, an indicator of primary productivity, in salt water is often far lower than predicted by freshwater phosphorus models (Campbell and Prepas 1986). Studies of marine (Howarth 1988), coastal pond (Caraco et al. 1987) and prairie saline lake systems (Bierhuizen and Prepas 1985, Campbell and Prepas 1986) indicate that N availability becomes increasingly important in limiting phytoplankton growth as salinity increases. N limitation in these systems is largely due to low rates of planktonic N_2 fixation (Howarth et al. 1988b). Many estuaries and saline lakes with high available P concentrations lack the large populations of nitrogen-fixing cyanophytes typical of high P freshwater lakes (Howarth et al. 1988b, Marino et al. 1990). Previous explanations of low N_2-fixing cyanophyte densities in estuarine phytoplankton communities included turbulence (lack of anoxic microzones, Paerl et al. 1987, Paerl et al. 1995) and low bioavailabilities of the key trace nutrients molybdenum (Mo, Howarth and Cole 1985) and iron (Fe, Howarth et al. 1988a). Because many ions are conservative in seawater, marine water chemistries tend to be tightly linked with salinity and it is difficult to isolate the biological effects of individual components.

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[1] A version of this chapter has been submitted for publication. J. C. Evans and E. E. Prepas. Limnology and Oceanography.

Saline lakes can provide the chemical variability needed to test some of the above hypotheses. Marino et al. (1990) found that the ratio of sulfate (SO_4^{2-}) to Mo was a good predictor of the relative abundance of nitrogen-fixing cyanophytes in 13 SO_4^{2-}-dominated prairie saline lakes, and that Fe (measured as total Fe) did not limit phytoplankton growth. However, this study was based on correlations (rather than bioassays), assumed P was not limiting, did not distinguish between total and bioavailable Fe and ignored the possible effects of grazing zooplankton (Campbell and Prepas 1986).

I examined water chemistry and phytoplankton communities in 11 high phosphorus saline lakes in Alberta, Canada to examine whether:

1. Lake phytoplankton is phosphorus limited because much of P found is biologically unavailable.

2. Phytoplankton growth is controlled by low levels of inorganic N and a low bioavailability of Mo, which impairs nitrogen fixation.

3. Phytoplankton growth is controlled by low bioavailability of Fe.

3a. Low Fe bioavailability is a result of unusually high alkalinities in the lake water.

To test these hypotheses, phytoplankton biomass and species composition were determined and their relationships with measured N and P were evaluated, along with ^{32}P-PO_4 (orthophosphate) uptake experiments and APA. Phytoplankton nutrient status, N limitation, Mo-deficiency induced nitrogen limitation and Fe limitation were explored by direct measurement of seston nutrient ratios and N_2 fixation rates and through bioassay experiments. Zooplankton gut pigments and carbon demand were also examined to evaluate the potential effects of grazers on the phytoplankton communities.

3.2 Methods:

Field collection — Eleven lakes in east-central Alberta were selected based on their wide range of salinities (Bierhuizen and Prepas 1985, Marino et al. 1990), their location within a relatively small geographical area (Evans and Prepas in press) and accessibility. Eight of these lakes were sampled 7 to 8 times between early May and mid-September, 1994. The remaining

three lakes were sampled once in early August. Eight of the lakes were part of the 1987 study by Marino et al. (1990), the additional lakes (Fluevog , Thomas and Vernon lakes.) were added to provide a wider range of salinities. Sampling was performed at the site of maximum depth. Vertical temperature profiles were taken at 0.5-m intervals and Secchi depths were measured for each sampling date.

All of the lakes were well mixed and the trophogenic zone included the entire water column in all but two of the lakes. To avoid contamination from the bottom sediments of these shallow lakes, sampling was restricted to the top 0.5 m of the water column. Water samples for water chemistry, Chl *a*, phytoplankton biomass and nutrient bioassays were collected by hand with opaque 2-L Nalgene bottles 250 mL polystyrene bottles to reduce the risk of metal contamination from both sediment and sampling equipment. Sample bottles were completely filled with water, samples used to determine nitrogen fixation rate, APA and ^{32}P-uptake were kept at ambient air temperature, all other samples were kept on ice in the field, then stored at 4°C until analysed.

Zooplankton samples were collected with a 30-cm diameter plankton net fitted with a 64-µm Nitex mesh collector. For each sample, 2 to 5 vertical hauls of the top 0.5 to 1 m of the water column were pooled and stored on ice in 100-mL glass jars. Zooplankton gut pigments were determined on two sampling dates in August. Fifteen large grazers (*Daphnia* spp. for most lakes) were placed in a vial containing 8 mL of 80:15:5 acetone:methanol:water pigment extraction medium immediately after collection. Samples were kept on ice while in the field and subsequently stored at -20°C prior to analysis.

All water sample bottles were acid washed for 48 h in 50% nitric acid (HNO_3), rinsed five times with distilled-deionized water (DDW) then twice with lake water prior to sampling. No detectable levels of nitrate were found in the third DDW rinse.

Laboratory Analyses — Glass and plastic equipment used in bioassays or in the determination of trace metals was acid washed as described above. All analyses were

performed in duplicate at 20°C within 24 h of sampling unless specified otherwise. Dilutions were performed as needed to keep analyte concentrations within the linear ranges of the methods used.

Conductivity was measured at 25°C with a Radiometer CDM 83 conductivity meter and a 1-cm CDC 304 probe, while pH was determined with a Fisher Scientific Accumet 925 pH meter equipped with a glass electrode. Colour and turbidity were determined for samples collected July 7 with a Hellige Aqua Tester model 611A and a Hach model 2100A Turbidimeter.

Total phosphorus (TP) and total dissolved phosphorus (TDP) were determined in duplicate by the potassium persulfate method as described in Prepas and Rigler (1982). Soluble reactive phosphorus (SRP) was determined similarly to TDP, but without persulfate digestion (Murphy and Riley 1962).

Orthophosphate uptake rates were determined in Camp and Cooking on August 15 and in eight lakes from July 19 to 21 using a modification of the assay method of Lean and Rigler (1974) as described by Evans and Prepas (in press). Uptake experiments were started within 30 min of sample collection and continued for 5 to 10 h at lakeside and in the laboratory. Alkaline phosphatase activity (APA) was measured from July to September by the method of Hill et al. (1968) as modified by Pick (1987a) and Evans and Prepas (in press).

Inorganic N was determined as ammonium (NH_4^+) by the phenolhypochlorite method of Solorzano (1969) and as nitrate+nitrite (NO_3^-) by the cadmium-copper reduction method of Stainton et al. (1977), both on a Technicon autoanalyzer. Total Kjeldahl Nitrogen (TKN) was analysed as ammonia by the method of Solorzano (1969) on preserved samples subsequently digested by the sulphuric acid-copper sulphate method of D'Elia et al. (1977) as modified by Prepas and Trew (1983). Total Nitrogen (TN) was the sum of NO_3^- and TKN.

Nitrogen fixation rates were estimated for June to early August samples by an acetylene reduction technique described by Flett et al. (1976) with modifications: a 145 mL aliquot of lake water that had been kept at 20°C was dispensed into each of ten 150-mL serum bottles which were then capped and sealed. A plastic syringe equipped with an 18-G hypodermic needle was

used to add 10.0 mL of acetylene to eight of these bottles, which were then shaken briefly. Six of these bottles were immediately placed in a growth chamber and incubated at 25°C and 35-40 $\mu E/m^{-2}sec^{-1}$ for 4 h, with gentle shaking, then immediately placed into ice water and allowed to equilibrate in the dark for 1 h. A 1-mL syringe was used to inject 1.0 mL of 1.00% ethylene (in N_2, certified gas mixture, Linde Canada Inc.) into the last two (non-acetylene treated) bottles. These standards and the remaining two acetylene-treated samples (blanks) were immediately placed into ice water and equilibrated in the same manner as the incubated samples. Following the equilibration period, the chilled samples were shaken 10 to 12 times and 4 mL of gas was removed from the sample head space with a clean 5-mL syringe. This subsample was immediately injected into a Hewlett-Packard 5890 Series II gas chromatograph equipped with a gas injection port (0.5-mL injection loop), a 3.2-mm x 2 .0-m Porpak-N column (8-100 mesh), and a flame ionization detector. A gradient temperature program of 70 to 130°C and a helium carrier gas pressure of 80 psi were achieved good separation of acetylene and ethylene, the two analyte gases. Blanks were used to determine the initial concentrations of ethylene present in the gas head space (due to the presence of trace levels of ethylene in the acetylene injected). Both blank and standard values were determined for each lake, since the large variation in salinity from lake-to-lake caused some variation in lakewater gas solubility and thus variation in the gas phase:aqueous phase partition ratios.

Alkalinities were determined by potentiometric titration with 0.5 N H_2SO_4 on a Mettler DL 21 autotitrator equipped with a glass electrode. All other ions were determined on samples that had been filtered through HNO_3-washed, DDW-rinsed 0.45-µm Millipore HAWP membrane filters. SO_4^{2-} and chloride (Cl^-) were analyzed on a Dionex 2000i/SP ion chromatograph fitted with an AS4A-Sc high capacity anion exchange column, samples for major cations (Na^+, K^+, Ca^{2+} and Mg^{2+}) were acidified to pH<2 with concentrated HNO_3 and analysed on a Perkin Elmer 3300 atomic absorption spectrophotometer. Na^+ and K^+ were analysed by atomic emission, Ca^{2+} and Mg^{2+} by atomic absorption, all with an air-acetylene flame (Environment Canada 1979, Ingle and Crouch 1988).

Total Fe was determined by flame atomic absorption on samples that had been acidified to pH < 1.5 with concentrated HNO_3. Samples for dissolved iron were filtered within 8 h of sampling, acidified to pH < 1.5 with concentrated HNO_3 and analysed on a graphite furnace equipped Perkin Elmer 3030 atomic absorption spectrophotometer (GFAAS).

Dissolved molybdenum was determined by coprecipitation of triplicate 75-mL aliquots of filtered lakewater with MnO_2 and subsequent analysis of the redissolved precipitate by GFAAS (Marino et al 1990). In an earlier study of Alberta saline lakes (Marino et al. 1990), molybdenum concentrations were constant throughout the growing season, therefore this parameter was measured only in spring.

Dissolved organic carbon (DOC) was measured in August 2 samples that had been filtered through precombusted Whatman GF/F filters. DOC was measured in acidified (pH 2), sparged subsamples on an Ionics Corporation 1505 programmable carbon analyzer at 850°C with a platinum catalyst.

Protein and carbohydrate were measured on seston obtained by filtration of pre-screened (243-μm mesh) lake water through precombusted 4.25-cm Whatman GF/F filters within 24 h of sampling. Seston samples were then kept frozen until analyzed. Aliquots were 10 -100 mL each, depending on phytoplankton densities. Particulate carbohydrate was measured as μg glucose equivalents per litre with the phenol-sulphuric acid method of Pick (1987b), modified for a Milton-Roy 1001 spectrophotometer with 10-mL cells. Particulate protein was extracted as described by Pick (1987b) and measured as μg bovine serum albumin equivalent protein L^{-1} after Lowry et al. (1951), modified for 10-mL spectrophotometer cells. Seston protein:carbohydrate ratios were interpreted as indicators of nutrient deficiency according to Pick (1987) and Waiser and Robarts (1995). Ratios of protein:carbohydrate over 1.2 indicated no nutrient deficiency, ratios below 0.7 indicated severe nutrient deficiency.

Particulate carbon (PC), nitrogen (PN) and phosphorus (PP) were determined on seston collected on precombusted 2.5-cm Whatman GF/F filters within 24 h of sampling. Lakewater aliquots (2.0 to 50 mL each) were filtered under gentle vacuum, rinsed once with 5 mL of 2%

H_2SO_4 to remove mineral carbonates and phosphates, and twice with DDW to remove dissolved P. PC and PN were analysed on a Control Equipment Corporation 440 elemental analyser after Environment Canada (1979). Certified CHN content acetanilide (Exeter Analytical Inc.) was used as a standard. In the case of Camp, Cooking and Miquelon lakes, where TDP was low compared to TP, PP was calculated as TP -TDP. In the remaining lakes, where the TDP was > 75% of TP, separate analysis of the seston was necessary. Seston samples for PP were added to 50 mL DDW and analysed as for TP. Samples were centrifuged after reagent addition to remove the glass filter fibres before measurement of absorbance. Particulate elemental concentrations were converted to moles per litre lake water and the composition ratios; PC:PN, PC:PP, and PN:PP were calculated and compared with those predicted by Redfield (1958), without correcting for detritus. Seston PC:PP ratios > 106 and PN:PP ratios > 16 indicated P-deficiency and PC:PN ratios > 6.6 indicated N-deficiency. (Waiser and Robarts 1995).

Chl *a* was determined in triplicate in seston collected (within 8 h of sampling) by vacuum filtration on Whatman GF/C filters which were then frozen and protected from light until analysed. The filters were subsequently extracted (within 3 wk) with 95% ethanol and Chl *a* was measured on a Milton Roy Spectronic 100+ spectrophotometer following Bergmann and Peters (1980).

Subsamples for phytoplankton determinations were preserved within 6 h of sampling with Lugol's iodide, subsequently identified to species (where possible) and counted on an inverted microscope by the sedimentation technique (Lund et al. 1958). Biovolumes were estimated with average (at least 10 cells) cell volumes for each species observed and were determined separately for each sample. The biovolumes of large diatoms and some colonies (such as *Pediastrum* spp.) were determined on an individual basis. Additional Lugol's solution was added to the stored samples periodically, because the iodine added to the saline lake water was chemically reduced over time.

Zooplankton were anaesthetized with carbonated water, which caused them to sink to the bottom of the sample, and the supernatant containing the phytoplankton was removed. The zooplankton were then filtered onto 64-μm Nitex mesh, gently rinsed with DDW to

remove lake salts, placed in pre-dried, pre-weighed porcelain dishes and oven-dried at 60°C for 24 h. After cooling in a dessicator, samples were weighed on a Mettler AT261 Delta Range electronic balance (±.0.02 mg). Zooplankton wet weight was calculated as 8.33 times the dry weight (Taguchi and Fukuchi 1975). The presence of characteristic pigments in the zooplankton gut extract was used to qualitatively identify the phytoplankton taxa ingested (Quiblier et al. 1994). Pigment signals were classified as strong or weak to semi-quantify the relative importance of the phytoplankton groups in the zooplankton diet. Zooplankton pigment extracts were filtered through 0.2-μm Acropore membrane filters, dried with a stream of nitrogen gas and stored under nitrogen at -20°C until analysis (Leavitt et al. 1989). Pigment determinations were made by reverse-phase high performance liquid chromatography (HPLC) following the method of Leavitt and Findlay (1994).

Bioassays — Laboratory bioassays were used to determine factors potentially limiting phytoplankton growth in the lakes, as indicated by increased Chl *a* with respect to controls. Lake water that had been kept at 4°C, an algal inoculum and the bioassay treatment were placed in 150-mL Wheaton Type 1 borosilicate glass serum bottles and incubated at 23°C under incandescent lights (16 h light, 8 h dark cycle, 35-40 $\mu E \cdot m^{-2} \cdot sec^{-1}$) with gentle shaking (≈ 2 Hz). Samples were shaken thoroughly every two d to reduce clumping and incubated for 14 d prior to Chl *a* analysis; one experiment ran for 35 d. Experimental treatments were run in triplicate, with a single Chl *a* analysis per replicate. All lakewater aliquots were pre-screened through 64-μm Nitex mesh to remove zooplankton. The inoculum, which was added to all treatments, consisted of native algae grown in 500 mL untreated, pre-screened lake water (prepared separately for each lake) for 1 month. Seeding bioassays with "enriched" native algal populations eliminated the problem of highly variable growth between replicates (caused by low cell numbers in the lakewater). Inorganic-N limitation was tested in water from all study lakes with NH_4Cl and $CaNO_3$ (250 $\mu g \cdot L^{-1}$ N), P limitation was tested in lakes with SRP < 100 $\mu g \cdot L^{-1}$ (Camp, Cooking and Miquelon) by an addition of K_2HPO_4 (250 $\mu g \cdot L^{-1}$ P). Trace nutrient limitation was examined with

treatments of Mo (240 $\mu g \cdot L^{-1}$ Mo as Na_2MoO_4), Fe (1300 and 250 $\mu g \cdot L^{-1}$ as ferric ammonium citrate and 1300 $\mu g \cdot L^{-1}$ as $FeCl_3$), the chelating agent ethylene diamine tetraacetic acid (EDTA, 12 $mg \cdot L^{-1}$), and a trace element solution (170 $\mu g \cdot L^{-1}$ B, 500 $\mu g \cdot L^{-1}$ Mn, 60 $\mu g \cdot L^{-1}$ Zn, $\mu g \cdot L^{-1}$ Cu, 5 $\mu g \cdot L^{-1}$ Co) both as single treatments and in combination. Since Mo deficiencies are known to interfere with the use of NO_3^- as a source of inorganic N (Alexander 1977), Mo was also tested in combination with NO_3^-. To ensure that the reagents and glassware used in the bioassays were free of Mo contamination (which would make detection of Fe-Mo co-limitation impossible), the Fe and trace metal solutions were added to Mo-deficient cultures of *Anabaenopsis* sp. in the concentrations used in the bioassay treatments. Reagent additions did not relieve Mo deficiency in the test organism, which could not fix N_2 nor grow in N-deficient media without added Mo solution (Evans, unpublished data). The effects of filtering the lake water (0.45-µm) and partial acidification (25% and 50% of total alkalinity removed) of the sample with H_2SO_4 were also examined. A one-way analysis of variance (SPSS) was used to test for significant ($P < 0.05$) differences between treatments.

3.3 Results

Physical characteristics, nutrient and ion chemistry — Mean seasonal lakewater conductivity ranged from 1.83 to 58.8 $mS \cdot cm^{-1}$ and mean seasonal pH from 9.15 to 9.98 (Table 3.1), the two parameters were positively related ($n = 11$, $r^2 = 0.83$, $P < 0.0001$). There was little seasonal variation in lake Secchi depth: mean seasonal values ranged from 0.14 to 2.75 m. In Camp and Cooking lakes, the low Secchi depths (0.14 and 0.26 m) reflect high Chl *a* concentrations, while high levels of suspended particles and colored dissolved material were important influences on light extinction in the other study lakes (Table 3.1).

Lake ion chemistry was dominated by Na^+, SO_4^{2-}, and $HCO_3^- - CO_3^{2-}$ (Table 3.2) mean seasonal concentrations of these ions were correlated with lake conductivity ($n = 11$, $r^2 = 0.93$, 0.86, 0.68 and 0.95 respectively, $P < 0.005$). Other conservative ions (K^+, Cl^-) were less concentrated in these lakes (33 - 562 and 15 - 1070 $mg \cdot L^{-1}$). Concentrations of Ca^{2+} were

Table 3.1: Location and general features of the study lakes.

Lake	Coordinates (°N)	(°W)	Area (km^2)	Max. depth (m)	Conductivity * ($mS \cdot cm^{-1}$)	pH *	Color ** (mg $Pt \cdot L^{-1}$)	Turbidity (NTU)**
Birch	53°21'	111°32'	3.0	4.5	29.6	9.64	40	5
Camp	53°05'	111°32'	1.4	4	2.06	9.28	20	12
Cooking	53°25'	111°05'	19	2.6	1.83	9.29	50	41
Fluevog +	52°50'	111°19'	0.3	2.1	17.9	9.63		
Joseph	53°17'	111°04'	5.9	3	3.5	9.15	30	11
Miquelon	53°15'	112°55'	7.8	4	7.16	9.45	20	4
Peninsula +	52°52'	111°29'	1.4	3.1	14.2	9.54		
Thomas	53°05'	111°42'	4.6		16.6	9.39	50	10
Vernon +	52°57'	111°25'	10.9	0.5	58.8	9.92		
Wappa	53°22'	111°37'	1.0	2	4.38	9.32	70	19
Whites	53°21'	111°39'	4.0	1.5	8.48	9.43	120	15

+ Sampled Aug. 2 only
* mean seasonal value
** July 7 value
A blank entry denotes a parameter that was not measured for the indicated lake.

Table 3.2: Mean 1994 growing season nutrient and major ion concentrations in the 11 study lakes.

Lake	TP	TDP	SRP	TN	TKN	DOC	Na^+	K^+	Ca^{2+}	Mg^{2+}	Cl^-	SO_4^{2-}	HCO_3^-	CO_3^{2-}	Mo	Total Fe	Fe (< 0.45 um)
	$mg \cdot L^{-1}$	$mg \cdot L^{-}$	$mg \cdot L^{-}$	$mg \cdot L^{-}$	$mg \cdot L^{-}$	$mg \cdot L^{-}$	$mg \cdot L^{-1}$	$mg \cdot L^{-}$	$mg \cdot L^{-}$	$mg \cdot L^{-}$	$mg \cdot L^{-}$	$mg \cdot L^{-1}$	$mg \cdot L^{-1}$	$mg \cdot L^{-}$	$ug \cdot L^{-1}$ *	$ug \cdot L^{-1}$ ***	$ug \cdot L^{-1}$ **
Birch	24.2	23.4	23.2	10.06	9.98	195	10400	240	3.65	46.3	590	12890	5370	3700	6.8	1150	19.2
Camp	0.150	0.031	0.017	6.92	6.80	63	428	43.9	6.14	113	15.3	271	928	312	1.6	55	1.1
Cooking	0.428	0.060	0.012	12.35	12.33	99	343	59.8	19.4	68.4	26.8	479	496	218	2.3	510	4.4
Fluevog +	1.75	1.51	1.30			110	4490	120	8.40	100	226	6690	1960	1070			
Joseph	1.54	1.47	1.36	7.04	6.97	40	841	76.2	16.3	77.8	49.8	856	1020	278	4.1	770	<1.0
Miquelon	0.220	0.192	0.150	6.41	6.40	110	1810	92.0	5.28	247	101	2678	1230	539	2.0	140	3.7
Peninsula +	3.76	3.64	3.59			93	4130	82.5	4.71	83.6	220	4420	1750	960			
Thomas	11.3	10.8	10.8	5.44	5.43	77	5290	102	13.0	60.7	604	7780	1970	729	4.01	730	1.3
Vernon +	5.01	4.45	2.06			435	38800	562	2.94	89.5	1070	93100	4190	6400			
Wappa	2.18	2.09	2.05	3.75	3.73	58	1100	32.9	10.5	22.6	32.5	1040	1230	387	7.9	2800	5.2
Whites	7.52	7.32	7.27	4.86	4.80	86	2390	67.2	10.0	27.9	103	2280	1890	760	9.1	2550	1.9

+ Sampled Aug. 2 only
* May 3 value
** July 7 value
*** Aug. 15-16 value
A blank entry denotes a parameter that was not measured for the indicated lake.

comparatively low (2.94 - 19.4 $mg \cdot L^{-1}$) and tended to decrease with increasing lakewater conductivity, while Mg^{2+} concentrations varied considerably (23 - 247 $mg \cdot L^{-1}$) and were not related to conductivity ($r^2 = 0.0$).

Mean growing season TP and TKN were extremely high and relatively constant in most of the study lakes. Across the study lakes TP concentrations ranged from 0.150 to 24.2 $mg \cdot L^{-1}$, while TKN concentrations were within a smaller range of concentration (3.73 - 12.35 $mg \cdot L^{-1}$). TDP and SRP were also very high (normally > 75% of TP), except in Camp and Cooking lakes, where concentrations remained comparatively low and varied during the sampling period (Figure 3.1). Between 78-99% of TDP was present as SRP in the high P lakes, with the exception of Vernon Lake, where SRP made up only 46% of TDP.

NO_3^- and NH_4^+ concentrations varied throughout the growing season (Figure 3.2) in the eight major study lakes from below the detection limit (< 0.5 $\mu g \cdot L^{-1}$) to 422 and 386 $\mu g \cdot L^{-1}$, respectively. Only a small fraction (< 2%) of TN was due to inorganic N.

Concentrations of DOC were very high in all of the lakes (40 - 435 $mg \cdot L^{-1}$) but were not related to lakewater color. Total iron was also high (55 - 2800 $\mu g \cdot L^{-1}$) at the end of the growing season, however dissolved iron (< 0.45 μm) was low (<1.0 - 19.2 $\mu g \cdot L^{-1}$) during the summer. Spring dissolved molybdenum concentrations were high (1.6 - 9.1 $\mu g \cdot L^{-1}$) and, like total iron concentrations, were greatest in two lakes of medium salinity (Whites and Wappa).

Sestonic ratios and nutrient demands — APA and $^{32}P\text{-}PO_4$ uptake were measured as indicators of planktonic P-demand, while seston PC:PP, PN:PP and protien:carbohydrate ratios were used to evaluate seston P-deficiency or sufficiency. $^{32}P\text{-}PO_4$ uptake rates were negligible in all but the two least saline study lakes, Camp and Cooking. In these lakes, tracer uptake was so rapid that $^{32}P\text{-}PO_4$ turnover times could only be estimated as < 5 min for both the July and August experiments. Similarly, APA was below detection limit in all lakes but Camp and Cooking, where APA ranged from 2, 950 to 36,800 and 184 to 1820 nmol methylfluorescein·ug Chl $a^{-1} \cdot h^{-1}$, respectively. PC:PP ratios were indicative of severe P-deficiency (PC:PP > 106) in

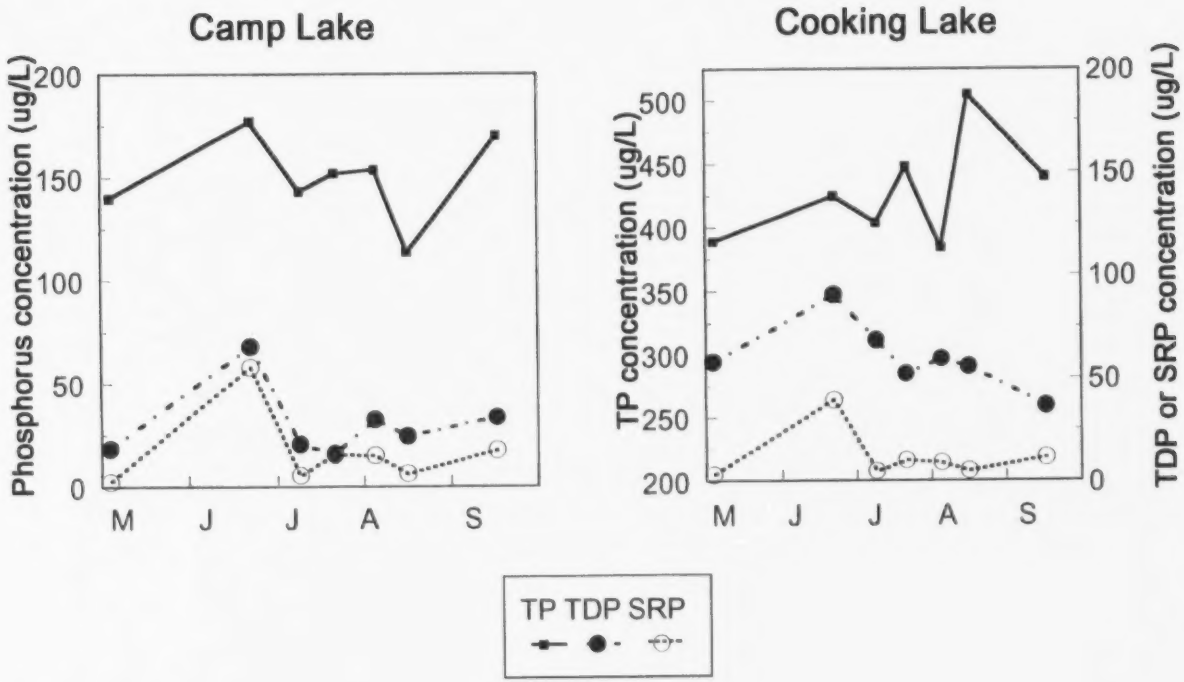

Fig. 3.1: May to September 1994 changes in total phosphorus (TP), total dissolved phosphorus (TDP) and soluble reactive phosphorus (SRP) in Camp and Cooking lakes. M J J A S = May, June, July, August and September.

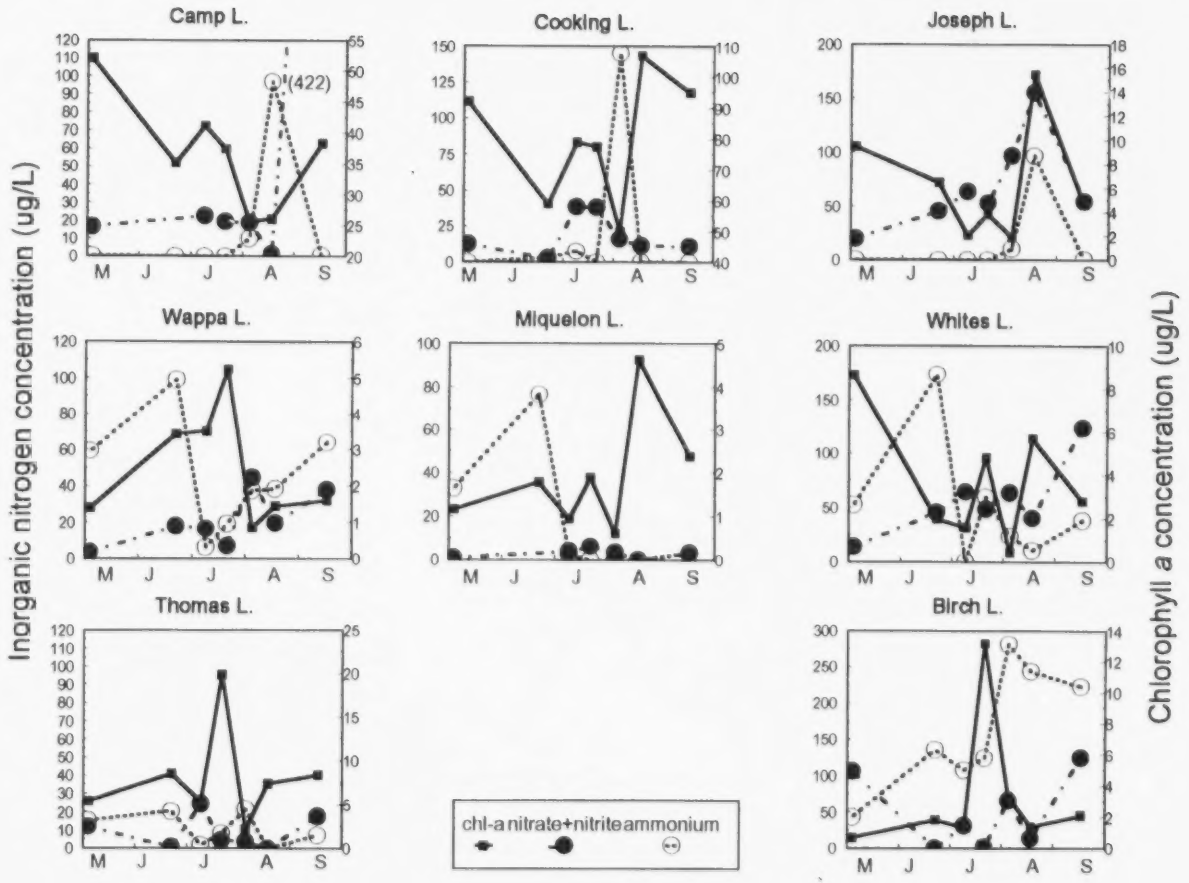

Fig. 3.2: May to September 1994 changes in chlorophyll *a* (Chl *a*), nitrate+nitrite and ammonium concentrations in the saline lakes. Lakes are shown in order of increasing lakewater conductivity. M J J A S = May, June, July, August and September.

Camp and Cooking lakes throughout the entire growing season (Table 3.3). P-deficiency was also indicated in the Vernon and Fluevog Lake samples and for at least one sampling date in each of the other study lakes, but was not indicated for the remaining samples. PN:PP ratios also indicated seston P-deficiency (PN:PP > 16) in Camp, Cooking, Fluevog and Vernon lakes, as well as deficiencies on two sampling days in Miquelon Lake, and one date in Whites Lake, but indicated no P-deficiency in Birch, Joseph, Thomas or Wappa lakes. The apparent inconsistency in the seston indicators of P-deficiency is due in part to a lack of nitrogen; seston PC:PN ratios indicated nitrogen deficiency (PC:PN > 6.6) in all seston samples.

Given this apparent universal nitrogen shortage, it was surprising to find that protein to carbohydrate ratios indicated severe nutrient deficiency (protien:carbohydrate < 0.7) only in Camp and Fluevog lakes, moderate deficiencies (0.7 < protein:carbohydrate < 1.2) in Cooking Lake and early-July Birch Lake and Thomas Lake samples and no deficiency at all in the remaining samples. Seston carbohydrate was highly correlated with PC (r = 0.88) and seston protein was almost perfectly correlated with PN (r = 0.99). It should be noted that seston ratios were determined with samples collected on GF/F filters and therefore represent combined phytoplankton and bacterial communities (larger bacterial cells and colonies), although the high correlation between seston protein and Chl a (see below) suggests that the bacterial protein contribution is either very low or itself tightly correlated to phytoplankton Chl a.

Nitrogen fixation was detected in only one sample (Thomas Lake, July 19, 62 nmol ethylene$\cdot L^{-1} \cdot h^{-1}$), and can be attributed to the heterocystous *Nodularia* sp. present in the lakewater. *Anabaena* spp. were also found in this sample, but lacked heterocysts. No nitrogen fixation was observed in Joseph Lake samples, despite the presence of nitrogen-fixing cyanophytes (*Aphanizomenon flos-aquae*, Fig. 3.3), however this may be due to the effects of sample transport on this species. In general, phytoplankton nitrogen demand appeared to be low or nonexistent, even though nitrogen deficiency was indicated by the lake seston ratios.

Table 3.3: Molar PC:PP, PC:PN and PN:PP ratios and mass-based protein:carbohydrate ratios in lake seston. PC:PP > 106 and PN:PP > 16 indicates P-deficiency, PC:PN > 6.6 indicates N-deficiency and protein:carbohydrate < 0.7 indicates nutrient deficiency.

Lake	Date	PC:PN	PC:PP	PN:PP	protein:carbohydrate
Birch	Jul-07	24.4*	98.8	4.1	1.05
	Jul-19	14.4*	78.5	5.5	1.18
	Aug-02	32.6*	70.9	2.2	2.39
	Aug-16				5.01
	Sep-13	25.5*	214*	8.4	0.84
Camp	Jul-07	13.7*	711*	52.1*	0.36*
	Jul-19	16.4*	591*	36.1*	0.47*
	Aug-02	18.1*	808*	44.6*	0.25*
	Aug-16				0.84
	Sep-13	12.3*	521*	42.3*	1.78
Cooking	Jul-07	12.3*	382*	31.2*	0.81
	Jul-19	12.8*	333*	26.0*	0.91
	Aug-02	13.8*	366*	26.4*	0.8
	Aug-16				0.91
	Sep-13	12.9*	424*	32.9*	1.13
Fluevog	Aug-02	9.1*	180*	19.7*	0.63
Joseph	Jul-07	12.0*	170*	14.1*	1.28
	Jul-19	10.9*	145*	13.2*	2.67
	Aug-02	17.5*	92.6	5.3	2.89
	Aug-16				2.44
	Sep-13	12.4*	87.8	7.1*	2.97
Miquelon	Jul-07	8.5*	87	10.2*	2.77
	Jul-19	13.7*	286*	20.9*	2.09
	Aug-02	15.0*	370*	24.6*	1.35
	Aug-16				2.38
	Sep-13	15.2*	132*	8.7*	1.75
Peninsula	Aug-02	14.7*	54.5	3.7	1.72
Thomas	Jul-07	15.5*	140*	9.0*	0.82
	Jul-19	10.5*	82.7	7.9*	1.23
	Aug-02	11.2*	101	9.1*	1.45
	Aug-16				1.61
	Sep-13	14.0*	139*	9.9*	1.97
Vernon	Aug-02	10.5*	434*	41.4*	2.17
Wappa	Jul-07	9.7*	135*	13.9*	1.32
	Jul-21	16.3*	118*	7.2*	1.20
	Aug-02	15.9*	36.8	2.3	1.88
	Aug-16				1.27
	Sep-13	22.4*	84.2	3.8	1.43
Whites	Jul-07	13.7*	244*	17.8*	1.30
	Jul-21	14.0*	59.1	4.2	2.16
	Aug-02	16.1*	11.4	0.7	1.99
	Aug-16				4.58
	Sep-13	27.8*	56.1	2.0	1.70

A blank entry indicates a parameter that was not measured for the indicated sample.
* value indicates nutrient deficiency

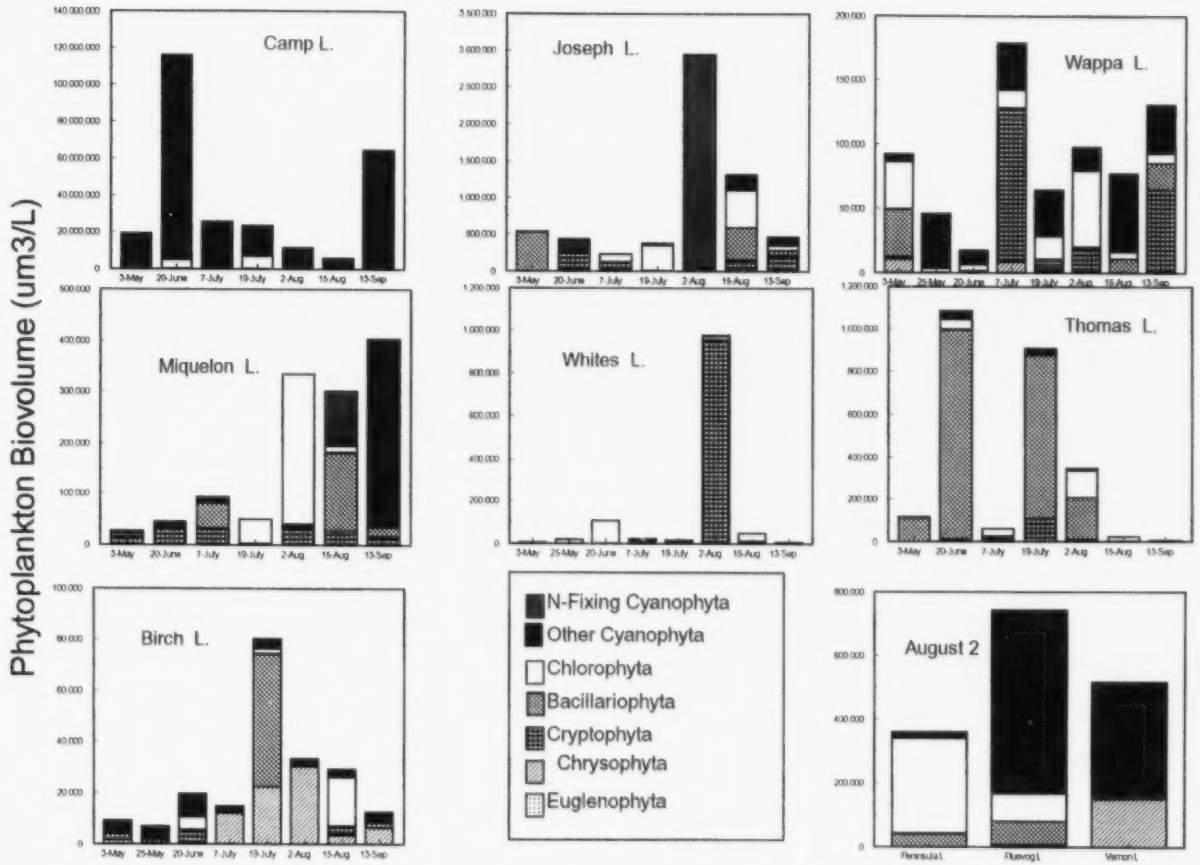

Fig. 3.3: May to September 1994 phytoplankton biovolumes and taxonomic compositions in the saline lakes. Lakes are shown in order of increasing lakewater conductivity. M J J A S = May, June, July, August and September.

Chl a and phytoplankton species composition — Chl *a* concentrations and phytoplankton biomasses varied considerably between lakes (Fig. 3.2), and varied somewhat seasonally, although patterns were not consistent from lake-to-lake. 61% of variation in phytoplankton biomass was explained by variation in Chl a, which also proved to be a good predictor of seston carbohydrate (r^2 = 0.69), protein (r^2 = 0.98) and particulate carbon (r^2 = 0.93).

The Camp Lake phytoplankton community consisted primarily of filamentous cyanophytes (non nitrogen-fixing), species composition remained relatively constant throughout the growing season. The phytoplankton communities in the more saline lakes were more variable (Fig. 3.3). The only nitrogen-fixing species found in the lakes were *Aphanizomenon flos-aquae*, primarily in Joseph Lake and *Nodularia* spp. and *Anabaena flos-aquae*, which were rare. The non nitrogen-fixing cyanophytes *Microcystis* spp., *Gomphosphaeria* spp. and *Merismopedia minima* were found in most of the lakes, while *Oocystis borgei* and *Crucigenia quadrata* were the most important chlorophytes. Diatoms (Bacillariophyta) were important in the lakes intermittently throughout the growing season and largely consisted of four genera: *Cyclotella*, *Surirella*, *Narvicula* and *Nitzchia*. *Rhodomonas minuta* and *Cryptomonas* sp. (Cryptophyta) were common in most of the lakes in July and August and unidentified, largely encysted, chrysophytes were important in the Birch, Wappa and Vernon phytoplankton communities (and found in small numbers in Thomas Lake). A species of *Euglena* (Euglenophyta) was found in small numbers in Thomas Lake. In general, cyanophytes were important in the low-salinity lakes, while diatoms, cryptophytes, and chrysophytes were common at higher salinities.

Zooplankton — Zooplankton wet weight was greater than phytoplankton biomass in Birch, Joseph (except Aug. 2), Miquelon, Thomas, Wappa and Whites lakes (Table 3.4). Zooplankton daily carbon demand, estimated as 0.8 ug C ug dry $wt^{-1} \cdot d^{-1}$ (Lampert 1977) could be supplied by seston carbon.

Zooplankton gut pigment analysis (Table 3.5) indicated that the large zooplankton present fed to some degree on phytoplankton. The presence of a strong cyanophyte signal in

Table 3.4: Comparison of 1994 zooplankton dry weight, wet weight and carbon demand (after Lampert 1977) with phytoplankton biomass and seston carbon supply (particulate carbon) in Alberta saline lakes.

Lake	Date	Zooplankton dry weight ($ug \cdot L^{-1}$)	Zooplankton wet weight ($ug \cdot L^{-1}$)	Zooplankton carbon demand ($ug \cdot L^{-1} \cdot d$)	Phytoplankton biomass ($ug \cdot L^{-1}$)	Seston carbon ($ug \cdot L^{-1}$)
Birch	20-Jun	353	2942	282	19.6	
	7-Jul	143	1192	114	14.8	1284
	2-Aug	246	2050	197	33.3	2290
	13-Sep	62.5	521	50	12.6	5638
Camp	20-Jun	107	892	86	116000	---
	7-Jul	73.3	611	59	25300	33940
	2-Aug	174	1450	139	11300	37940
	13-Sep	98.4	820	79	64800	27500
Cooking	20-Jun	524	4367	419	---	---
	7-Jul	875	7292	700	---	49730
	2-Aug	323	2692	258	---	45970
	13-Sep	125	1042	100	---	66380
Joseph	20-Jun	352	2933	282	430	---
	7-Jul	396	3300	317	225	2866
	2-Aug	283	2358	226	2945	2111
Miquelon	20-Jun	40.4	337	32	45.5	---
	7-Jul	35.9	299	29	93.3	911
	2-Aug	37.3	311	30	336	3298
	13-Sep	55	458	44	403	1385
Thomas	20-Jun	298	2483	238	1086	---
	7-Jul	98.9	824	79	61.2	4554
	2-Aug	79.4	662	64	349	4247
	13-Sep	62	517	50	5.7	3306
Wappa	20-Jun	84.7	706	68	17.5	---
	7-Jul	34.9	291	28	179	859
	2-Aug	58	483	46	98.0	2572
	13-Sep	23.6	197	19	131	2709
Whites	20-Jun	102	850	82	107	---
	7-Jul	42.7	356	34	21.5	1649
	2-Aug	55.3	461	44	978	2698
	13-Sep	29.6	247	24	8.1	2959

Table 3.5: Phytoplankton phyla representation in zooplankton diets as determined by qualitative analysis of crustacean gut pigments.

Lake	Date	Grazer*	Cyanophyta	Chlorophyta	Bacillariophyta	Cryptophyta	Chrysophyta**
Birch	Aug-02	large *Daphnia* spp.	strong	weak	weak	weak	
	Aug-02	Anostracans	weak				weak
	Aug-16	large *Daphnia* spp.	strong	weak		weak	
Cooking	Aug-02	small *Daphnia* spp.	weak	weak	strong	weak	
	Aug-16	N/A					
Joseph	Aug-02	large *Daphnia* spp.	strong	strong	weak	weak	
	Aug-16	large *Daphnia* spp.	weak	strong	weak	weak	
Miquelon	Aug-02	large *Daphnia* spp.	weak	strong	strong		
	Aug-16	large *Daphnia* spp.	strong	strong		strong	weak
Thomas	Aug-02	large copepods	Strong	strong	strong	weak	
	Aug-02	large *Daphnia* spp.	weak	strong		weak	
	Aug-16	large copepods	weak	strong		strong	
Wappa	Aug-02	large copepods	strong			weak	
	Aug-16	large copepods	strong	weak	weak	weak	
Whites	Aug-02	large *Daphnia* spp.	weak		weak	weak	
	Aug-16	large *Daphnia* spp.	weak			strong	

* each pigment extraction used 15 individuals, except Anostracans (3 individuals)

** Chrysophyte signal cannot be determined in the presence of a strong Bacillariophyte signal

"strong" refers to characteristic pigment signals > 50,000 microvolt-sec

"weak" refers to characteristic pigment signals between 5,000 and 50,000 microvolt-sec (detection limit approx. 1500 microvolt-sec)

A blank entry indicates that no characteristic pigment of the indicated phylum was found in the sample.

many of the samples indicates that members of this phylum, often considered to be "inedible", are subject to grazing pressure in these lakes, although it does not indicate whether they are subsequently digested. Some selective grazing appears to be taking place in that gut pigment signals do not always correspond to dominant phytoplankton phyla (e.g., Aug. 2 in Birch L., where chlorophytes, which are very poorly represented in the phytoplankton, are clearly represented in the zooplankton gut pigments).

Bottle bioassays — Nutrient addition experiments in the lakes indicated that Cooking lake water was limited by P (Fig 3.4), while lake water with TP > 1 mg/L (all other lakes except Camp and Miquelon) was limited by Fe (Fig. 3.5). Vernon Lake water also required a trace nutrient spike. Fe treatments caused massive growth in lake water and allowed almost complete exploitation of P present. NH_4^+ additions caused increases in Chl *a* only in Joseph and Fluevog lake water (Fig. 3.4), while no changes were observed for NO_3^- or NO_3^-+Mo additions. Mo (Fig 3.4), trace nutrient (Fig. 3.5) or EDTA (Fig 3.6) additions likewise had no effect. Partial acidification of the sample (titration of 25% or 50% of the total alkalinity) had the same effect as the Fe addition in Fe-limited lakes (Fig. 3.6). In water from Birch, Thomas, Wappa and Whites lakes, reducing alkalinity by 1/4 caused increases in phytoplankton biomass, while Joseph Lake phytoplankton responded only when a greater proportion (1/2) of the lakewater alkalinity was neutralised.

Removal of particulate Fe by filtering (0.45 μm) the lake water prior to seeding reduced growth with respect to the controls in water from Joseph, Whites, Birch (Fig. 3.6) and Wappa lakes (Fig. 3.7). The reduction in biomass was not significant in Thomas Lake. Experiments with Wappa and Birch lake water indicated that growth in the filtered lake water was increased by Fe additions, while partial acidification of the filtered lake water increased growth significantly in Birch Lake only. Fe source (ferric ammonium sulfate vs. $FeCl_3$) made no difference to the bioassay response (Fig. 3.7) and while there was some indication of a dose-response effect (1300 vs. 250 μg/L Fe) in water from both lakes, it was only significant for Birch Lake (Fig 3.7).

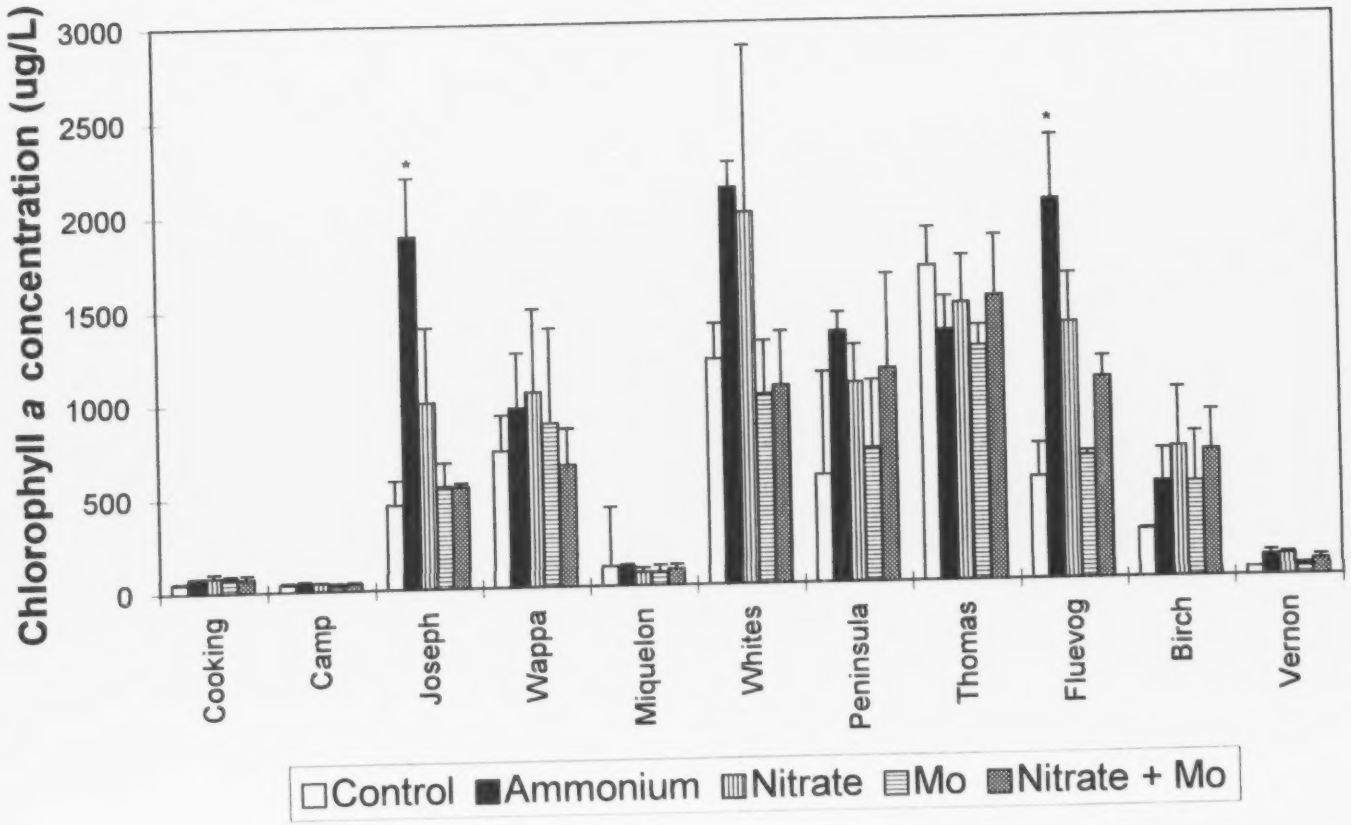

Fig. 3.4: Chlorophyll *a* concentrations 14 days post inoculation in saline lakewater bioassays with ammonium, nitrate, molybdenum and molybdenum+nitrate additions. Error bars = one standard deviation. *different from control ($P < 0.05$). Lakes are in order (from left to right) of increasing lakewater conductivity.

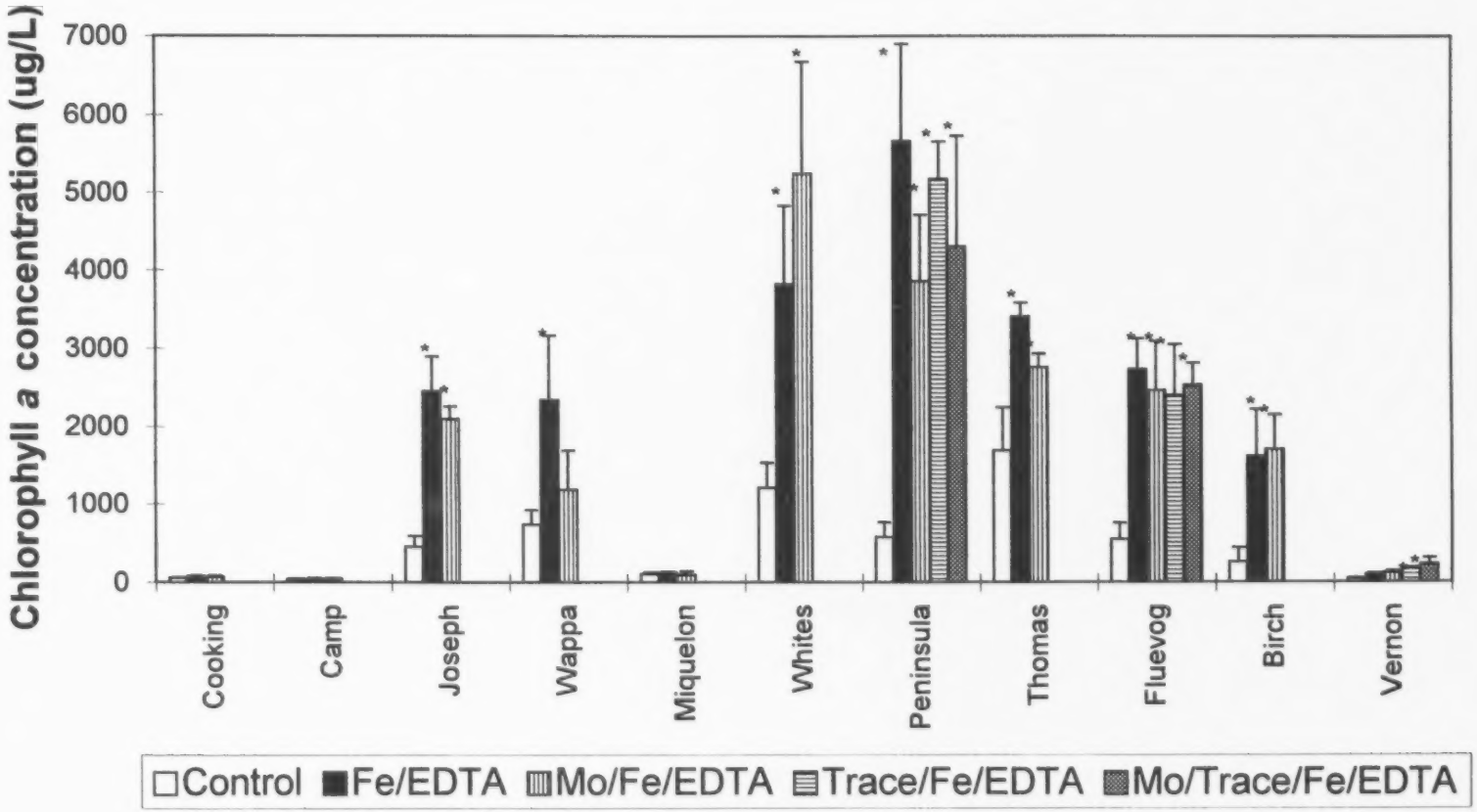

Fig. 3.5: Chlorophyll *a* concentrations 14 days post inoculation in saline lakewater bioassays with iron+EDTA, molybdenum+iron+EDTA trace elements+iron+EDTA and trace elements+molybdenum+iron+EDTA additions. Error bars = one standard deviation. *different from control ($P < 0.05$). Lakes are in order (from left to right) of increasing lakewater conductivity.

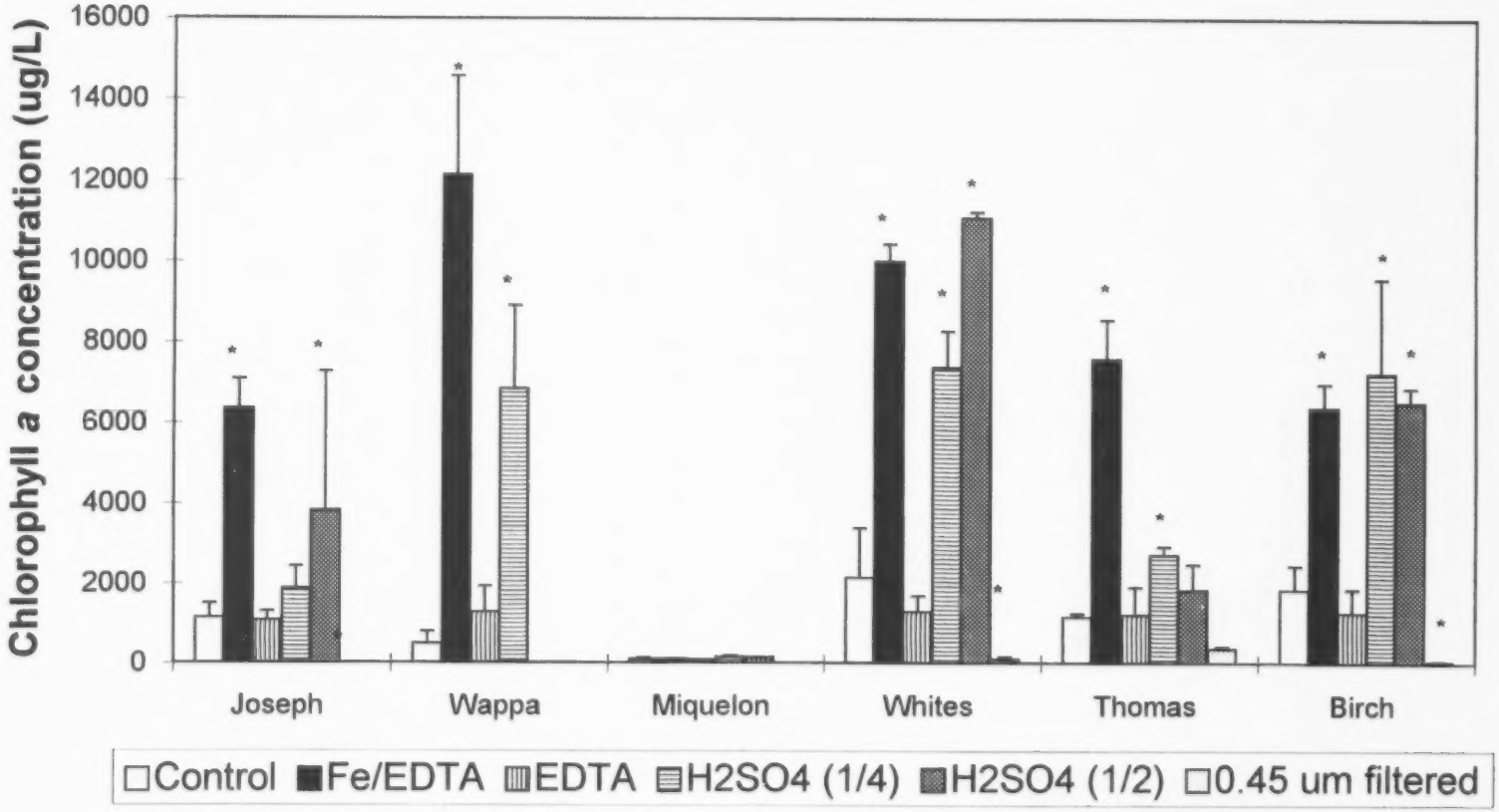

Fig. 3.6: Chlorophyll *a* concentrations 14 days post inoculation in saline lakewater bioassays with iron+EDTA and EDTA additions and 25% acidification, 50% acidification and 0.45 μm filtration manipulations. Error bars = one standard deviation. *different from control ($P < 0.05$). Lakes are in order (from left to right) of increasing lakewater conductivity.

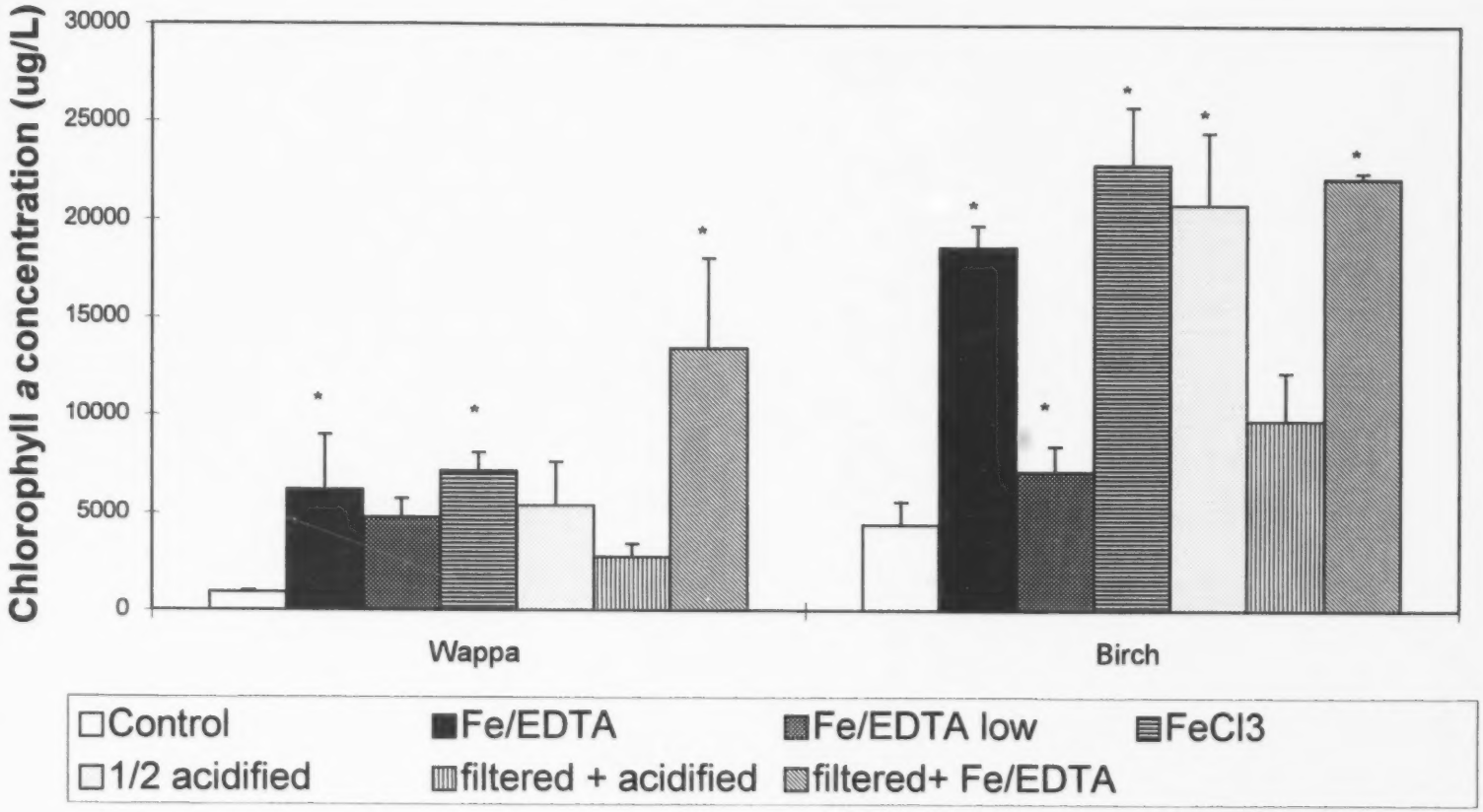

Fig. 3.7: Chlorophyll *a* concentrations 35 days post inoculation in saline lakewater bioassays with iron+EDTA, low (20% of normal dose) iron+EDTA and unchelated iron additions and 50% acidification, 0.45 μm filtration+acidification and filtration+iron+EDTA manipulations. Error bars = one standard deviation. *different from control ($P < 0.05$). Lakes are in order (from left to right) of increasing lakewater conductivity.

Miquelon Lake water did not respond to any bioassay treatment and may be limited by a combination of nutrients (such as P and Fe) not examined in the bioassays.

High concentrations of bioassay vs. *in situ* Chl *a* in the control treatments of all bioassays (except those with P-limited Camp or Cooking lake water) can be attributed to an increase in the amount of Fe available. This "bottle effect" is reduced dramatically when particulate (> 0.45 μm) Fe is removed by filtration. The phytoplankton growing in the bioassay experiments (except in Camp and Cooking Lake water bioassays) consisted almost exclusively of heterocystous nitrogen-fixing cyanophytes (primarily *Nodularia* and *Anabaena* spp.), with large numbers of heterocysts. The predominance of nitrogen-fixing species in the bioassays reinforces the idea that the lake phytoplankton were N-limited.

3.4 Discussion:

P and N limitation — Rapid $^{32}P\text{-}PO_4$ uptake, high APA (APA), extremely high PC:PP and PN:PP ratios and low seston protein:carbohydrate ratios indicate that the plankton communities in Camp and Cooking lakes were phosphorus limited. There were no signs of P-demand in the other lakes, indicating that the more saline lakes were P-sufficient. The lack of a response to P-addition in the Camp Lake bioassay may be due to binding of the added P with a fraction of the DOC pool. If the high levels of DOC present in the lake were constraining P availability, as suggested for two alkaline, Saskatchewan saline lakes (Waiser and Robarts 1995), the low concentration of Chl *a* (relative to those expected from TP levels, Prepas and Trew 1983) may be explained. The extremely high APA observed in Camp Lake (up to 36,800 nmol methylfluorescein ug Chl a^{-1} h^{-1}) in the presence of detectable SRP (Fig 3.1) also suggests that phosphorus availability is restricted. If the kinetics of DOC binding to P are sufficiently slow, tracer uptake experiments would not be affected. DOC binding to P is unlikely to restrict P availability in most of the high phosphorus (TP > 1 mg L^{-1}) lakes in the same way as suggested for the Saskatchewan systems because, although DOC concentrations in the study lakes are similar to those found by Waiser and Robarts (1995), phosphorus concentrations are far greater

in the Alberta lakes (up to 24.2 mg L^{-1} in Birch Lake vs.0.1 mg L^{-1} in Redberry Lake, Saskatchewan) An exception may be Vernon Lake, which has high DOC (435 mg L^{-1}) and comparatively low TP (5 mg L^{-1}) concentrations. DOC-P binding could account for the large difference (> 2 mg L^{-1}) between TDP and SRP in this lake (Table 3.2).

Although the phytoplankton assemblage of Joseph Lake alone was typical of N-limited systems, N limitation was undoubtedly a key factor in the low productivity of these lakes. The large DOC pools (and consequently, the large dissolved organic N pools) are refractory in Alberta saline lakes (Curtis and Prepas 1993) and are likely unavailable as a source of N. The TN:TP ratios used to predict the dominance of key phytoplankton phyla in freshwater systems (Smith 1982) are therefore of little value in these saline lakes, and models based on TN:TP ratios were poor predictors of Chl *a* concentration in Alberta saline lakes (Bierhuizen and Prepas 1985). Low concentrations of NO_3^- and NH_4^+, of which a considerable proportion was present as NH_3 at the high pHs (9.15 to 9.92) of these lakes, and high concentrations of SRP (1.3 to 23.2 mg L^{-1}) are generally indicative of N-limited systems (Howarth and Marino 1990), although the intermittent presence of higher concentrations of inorganic N (Fig. 3.2) is inconsistent with a high degree of N-starvation. High seston PC:PN ratios are also indicative of N-limitation. The lack of a significant response to NO_3^- additions in the bioassay experiments, even when combined with Mo, indicates that N is not the only factor limiting phytoplankton growth. Although it may be argued that phytoplankton response to the 250 $\mu g \cdot L^{-1}$ N addition was not large enough to overcome the scatter seen in the bioassays, a similar dose of NH_4^+ resulted in significant Chl *a* increases in water from two of the study lakes. This response may be due to a chemical property of NH_4^+/NH_3; NH_4^+ may compete with Fe for binding sites, NH_3 acts as a ligand for many trace metals.

Mo and Fe limitation — Marino et al. (1990) found evidence of SO_4^{2-}-induced Mo limitation in a group of 13 Alberta lakes, eight of which were examined in this study. The Marino et al. study modelled the relative importance of nitrogen-fixing cyanophytes in lake phytoplankton as a

function of lake conductivity, SO_4^{2-}, total Fe, dissolved Mo or SO_4^{2-}:Mo ratio alone as well as multiple regressions with Mo and SO_4^{2-} or Mo and conductivity (with and without Fe) and reported that only interactions between Mo and conductivity or SO_4^{2-} were correlated with nitrogen-fixer abundance. Of the eight lakes examined in both studies, water from two (Camp and Cooking lakes) was P limited in 1994 with no evidence of N_2 fixation; N supply was probably sufficient to meet phytoplankton needs in the two lakes (although PC:PN ratios suggested otherwise). Comparisons of 1987 and 1994 SO_4^{2-}:Mo ratios and relative proportion of planktonic nitrogen fixers in water from four of the study lakes indicates that this relationship changed between 1987 and 1994. Although the SO_4^{2-}:Mo ratio decreased from 2.5 to 2.1 $x10^5$ in Joseph Lake and the importance of N_2-fixing cyanophytes increased (0.43% in 1987 to 63% in 1994, Fig. 3.3), the May to August average phytoplankton biovolume was more than an order of magnitude lower in 1994 than in 1987. The SO_4^{2-}:Mo ratio (1.2 to 1.3 $x10^6$) increased slightly in Miquelon Lake as did the proportion of nitrogen-fixing cyanophytes (0 to 11%). In contrast, SO_4^{2-}:Mo ratios decreased in Whites and Wappa lakes (3.4 to 2.5 $x10^5$ and 2.2 to 1.3 $x10^5$, respectively) from 1987 to 1994, but the proportions of phytoplankton able to fix nitrogen decreased drastically (to 50% and 49% to 1.5 and 0.3%, respectively) over the same time period. Similarly, May to August 1994 average phytoplankton biovolumes were far lower than in 1987; 0.34% of the Whites and 0.06% of Wappa 1987 phytoplankton biovolumes were found in 1994.

Molybdenum additions had no effect on the concentrations of Chl a in bioassays either with or without nitrate (Fig. 3.4), while additions of molybdenum with iron and a trace nutrient solution had the same effect as iron alone (Fig. 3.5).

Although the inhibitory effect of SO_4^{2-} on uptake of the structurally similar molybdate (MoO_4^{2-}) anion is well documented for mammals, bacteria and higher plants as well as phytoplankton (Cole et al. 1986), it is not responsible for limiting N_2 fixation in Alberta saline lakes. Even though Mo uptake rates in lake phytoplankton are probably slowed due to competition with SO_4^{2-}, the biological demand for Mo may be so low that overall changes in growth rates are well below detection. Luxury uptake and storage of Mo during periods of low growth or high Mo availability may also be important in alleviating the effects of reduced uptake

rates (Ter Steeg et al. 1986). Similar results were reported for marine N_2-fixing cyanophytes present in intertidal microbial mats (Paerl et al. 1987); SO_4^{2-} and Mo additions had no effect on N_2-fixation rates and responses to mannitol additions indicated that these systems were not limited by Mo.

Iron was clearly the key factor in controlling growth in the bioassays (Figs. 3.5 and 3.6) of the high P (TP > 1 mg·L) study lakes. Increases ($P < 0.05$) in Chl *a* concentration, compared to the controls, were found for Fe additions in four to five completely independent bioassays of Birch, Joseph, Thomas, Wappa and Whites lake water. Independent bioassays used lake water collected on different dates. Fe additions also increased Chl *a* concentration in the single bioassays of Fluevog and Peninsula Lake water, while phytoplankton in Vernon Lake water responded only to a combined Fe and trace nutrient addition. Earlier investigations in the Alberta saline lakes rejected Fe limitation as a factor in controlling phytoplankton growth on the basis that total Fe concentrations were very high (Marino et al. 1990) and no response was observed in bioassays with EDTA (Campbell and Prepas 1986). Measurements of total and "dissolved" (< 0.45 μm) Fe fractions indicated that the vast majority of Fe is present in particulate form (Table 3.2) and may not be bioavailable. EDTA additions did not increase the availability of Fe in the bioassays (Fig. 3.6), indicating that this traditional method of assessing Fe limitation is not valid for high pH saline lakes similar to those found in Alberta. The lack of response to EDTA may be due to high concentrations of other ions in the lake water, which compete for binding sites on both Fe and EDTA. The presence or absence of an added chelating agent did not modify the effects of Fe additions (Fig. 3.7). The "bottle effect" observed in the bioassays, which could be largely eliminated by removing particulate Fe (Fig. 3.7), may be the result of increased Fe availability on the glass surface (which may be competing with suspended particulates for adsorbed Fe - A.J. Horne; H. W. Paerl pers. comm.).

Some factor related to alkalinity (precipitation with phosphate, hydroxide or carbonate) appeared responsible for restricting Fe bioavailability. The phenomenon of alkalinity-induced Fe deficiency explains the dramatic changes in cyanophyte species abundances between 1987 and 1994 in Wappa and Whites lakes, which could not be explained by changes in the SO_4^{2-}:MoO_4^{2-}

ratios. Alkalinities in Wappa and Whites lakes, which were 8.8 and 11 meq/L, respectively, in 1987 (Marino et al. 1990) increased dramatically during the following years, coincident with increases in lakewater salinities (Evans and Prepas in press), to 33 and 56 meq/L, levels which were more typical of cyanophyte-free Birch Lake water in 1987. Increases in the alkalinity of Joseph Lake water (8.3 to 26 meq/L) were almost as great and may account for the massive decrease in phytoplankton biovolume from 1987 to 1994. The increase in relative importance of nitrogen-fixing cyanophytes observed in Joseph Lake is not accounted for by a reduction in Fe availability, however, since P concentrations were much lower in 1987 than in 1994, while biovolumes were more than 10 times as high, this lake may have been P limited in 1987. Inorganic carbon uptake in these shallow lakes is not likely pH limited, in contrast to the situation in saline Pyramid Lake (mean depth 59 m), where high lakewater pH is believed to restrict access to free carbon dioxide in all but the top 50 cm of the water column and therefore acts to limit N_2 fixation (Horne and Galat 1985).

It is interesting to note that there are indications of a dose-response effect even at the high Fe concentrations used in these experiments. Since any Fe added to lake water will be subject to the same chemical environment that restricts the bioavailability of Fe already present, large doses may be needed to overcome the inevitable loss of added nutrient. Phytoplankton response would then depend both on Fe dose and the rate at which added Fe is removed from solution. The high Fe dosage used in the bioassay experiments was similar to that used by Paerl et al. (1987) in a study of factors affecting N_2 fixation in marine microbial mats. N_2 fixation in these mats was unaffected by Fe dosage and increased N_2 fixation rates achieved when a sugar (mannitol) was added indicate that Fe was not limiting. The differences in responses of cyanophyte mats and cyanophyte phytoplankton may be due to the increased availability of Fe in benthic and mat environments - anoxic conditions in these systems tend to reduce metal ions and make them more bioavailable (Howarth et al. 1988a). Marine cyanophyte mats tend to have high rates of N_2 fixation (Howarth et al. 1988b), in contrast to marine phytoplankton, which lack access to this sediment mineral pool, and are therefore more likely to be iron deficient. Fe additions can increase N_2 fixation rates of marine planktonic *Trichodesmium* spp., both in

naturally occurring populations and in cultures grown in seawater (Paerl et al. 1994). Recent experiments in the high-NO_3^-, low-Chl *a* region of the Equatorial Pacific Ocean indicate that not only N_2 fixation, but phytoplankton growth in general is severely limited by Fe bioavailability in the open ocean (Martin et al. 1994) and this may also be the case in certain saline lakes. If Fe limitation is sufficiently severe in saline lakes that nitrogenase synthesis is restricted, the competitive advantages that N_2-fixing species normally have in nitrogen-restricted environments no longer exist. N_2-fixing cyanobacteria would then be expected to have low relative abundances in these lakes, which agrees with observations made in both 1987 (Marino et al.) and 1994 (Fig. 3.3).

Zooplankton grazing — Campbell and Prepas (1986) found that zooplankton grazing had no effect on Fluevog Lake Chl *a* in short-term (2 h) incubation experiments and suggested that bacteria made up a large proportion of the zooplankton diet in these lakes (although the bacterial and phytoplankton populations combined were still insufficient to meet the estimated carbon demand of the massive zooplankton community). The presence of phytoplankton pigments in zooplankton gut extracts (Table 3.5) indicates that phytoplankton (including Cyanophyta) in the lakes were grazed and, given that zooplankton biomass exceeded phytoplankton biomass (by up to 100x) in all but the two least saline lakes (Camp and Cooking lakes, Table 3.4), the effects of grazing were likely appreciable. The large seston carbon pools (Table 3.4) in the saline lakes are probably an important factor in maintaining grazer populations far in excess of those normally supported by similar phytoplankton biomasses in freshwater systems (Campbell and Prepas 1986). NH_4^+ excretion by zooplankton can also inhibit N_2 fixation (Roth and Horne 1981), a phenomenon which would reduce the ability of "inedible" N_2-fixing filamentous cyanophytes to succeed edible species during periods of intense grazing. Grazing pressure, possibly coupled with the side effect of NH_4^+ release, undoubtedly exacerbated low Fe bioavailability in limiting phytoplankton standing crops in these high-P lakes.

Low phytoplankton standing crops in the high P Alberta saline lakes thus appear to be the result of a combination of nutrient limitation and trophic factors not found as part of the

freshwater paradigm. Further explorations of Fe and P limitation in similar lakes with conductivities between those of P-limited Camp Lake and Fe-limited Joseph Lake are needed to determine the factors controlling the type and severity of nutrient limitation in a given system. The mechanisms of alkalinity-induced Fe limitation should be determined in both saline lakes and marine systems. Low Fe bioavailability in the ocean is currently believed to be a major factor limiting the growth of marine phytoplankton. Saline lakes can provide the chemical variability needed to explore this phenomenon outside the laboratory.

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Chapter 4

4.1: General discussion and conclusions

(1) *Impacts of climate change on Alberta saline lake chemistry.*

Decreases in precipitation/evaporation ratios during the 12-year study period resulted in increases in brine conductivity in the closed basin saline lakes of the study region. Overall, concentrations of sodium, potassium, magnesium, sulfate, chloride and alkalinity increased as predicted by Last (1992), although the relationship between magnesium and conductivity was weak in individual lakes. Calcium concentration decreased as salinity increased, indicating that Alberta lakes were saturated with calcium minerals, probably carbonates. Lake alkalinities were sufficiently large compared to calcium concentrations that they continued to increase by evapoconcentration despite the inevitable losses that must have occurred due to calcium carbonate precipitation. Hammer (1986b) describes the ratio between carbonate+bicarbonate and calcium+magnesium as an important factor in the brine evolution of these lakes; the highly alkaline water in lakes examined for this study are the result of a surplus of carbonate and bicarbonate anions.

Decreases in the relative proportions of alkalinity, calcium and magnesium are due to precipitation of carbonate minerals, while increases in the relative proportions of sodium, sulfate and/or chloride with conductivity also reflect the largely carbonate-driven brine evolution of these lakes. In lake water of relatively low alkalinity (alklainity < calcium+ magnesium) , precipitation of gypsum ($CaSO_4{\cdot}2H_2O$) acts to decrease the relative proportion of sulfate as salinity increases. In the study lakes, precipitation of carbonate minerals depletes the supply of calcium and sulfate continues to behave conservatively, as do sodium and chloride, which form highly soluble salts. This conservative behaviour was not observed for potassium, which decreased in relative importance with lake conductivity. This loss of potassium is probably due to absorption on active clay mineral surfaces, rather than precipitation: potassium salts, like sodium salts, are highly soluble (Hammer 1986a).

Salinity-driven changes in the proportions of the major ions are important only when brine conductivity > 4500 $\mu S\ cm^{-1}$. At lower conductivities, brine composition is highly variable and may be controlled by phytoplankton-induced changes in lakewater carbonate concentrations (the "white-out" events observed in some freshwater lakes during periods of high photosynthesis).

(2) *Influence of salinity on phytoplankton.*

Although alkaline saline lakes in other regions, such as the Ethiopian Rift Valley, are among the most productive aquatic systems in the world (Wood and Talling 1988), Alberta saline lakes tend to have very low phytoplankton standing crops (Bierhuizen and Prepas 1985, Campbell and Prepas 1986) compared to those predicted by freshwater models based on total phosphorus concentration. Low chlorophyll *a* (Chl *a*) concentrations can be linked to the small quantities of bioavailable nitrogen in these lakes and the comparative rarity of nitrogen-fixing cyanophytes that could make up this deficit. Cyanophyte species, which were expected to dominate the phytoplankton of these high phosphorus alkaline lakes, were replaced by chlorophytes, chrysophytes and cryptophytes at higher salinities. This change occurred despite the presence of large zooplankton communities which would be expected to reduce standing crops of the more "edible" phyla and promote cyanophyte dominance.

Chl *a* concentrations in Alberta prairie lakes were below those predicted by freshwater models even at low salinities (> 0.5 g L^{-1}, Prepas and Trew 1983). As lakewater conductivity increases further, Chl *a* decreases dramatically, even though phosphorus concentrations tend to increase with lake salinity. The low conductivity (approx. 3500 $\mu S\ cm^{-1}$) at which this salinity-related decrease in phytoplankton standing crop occurs has profound implications for the ecology of lakes in the study region. The increased aridity predicted for continental interiors under current climate-change scenarios (Ramathan 1988) will lead to the increased salinization of Alberta lakes and ponds. If precipitation in catchment basins falls below that needed to replace

losses from lake evaporation, many of the currently highly productive "fresh" water bodies may evapoconcentrate to the point where they become oligotrophic.

(3) *Nutrient limitation.* The absence of nitrogen-fixing cyanophytes in the more saline lakes is not due simply to low halotolerance: the major cyanophyte species found in freshwater Alberta lakes have been observed at salinities far greater than those of the study lakes (Hammer et al 1983). Under conditions where nitrogen is not the sole limiting nutrient, nitrogen-fixing species will be unable to take advantage of their ability to exploit available phosphorus in the absence of inorganic nitrogen. This will lead to low relative abundances of nitrogen-fixing species, as well as overall low phytoplankton standing crops, as was observed for the more saline (lake water conductivity > 3 mS cm^{-1}) study lakes.

Phytoplankton in the two least saline lakes were limited by phosphorus; these lakes were also the most productive of the study lakes. With one exception, phytoplankton in lakes with conductivities > 3.5 mS cm^{-1} were all limited by low iron bioavailability, despite high total iron content of the lake water. In these lakes, iron bioavailability was controlled by some aspect of lakewater alkalinity, possibly by precipitation with carbonates, hydroxides or phosphates. The role of alkalinity in restricting the availability of iron needs to be examined further, as the same mechanism may be limiting iron bioavailability, and thus primary production, in marine systems (Martin et al. 1994). Sulfate-linked limitation of molybdenum uptake was clearly not a factor in limiting phytoplankton standing crop, as was concluded in an earlier study (Marino et al. 1990).

There appear to be two major influences of salinity on nutrient limitation in the study lakes. At low conductivities (< 3 mS cm^{-1}), Chl *a* concentrations are slightly less than predicted by freshwater phosphorus models, as observed by Prepas and Trew (1983) in lakes with TDS > 0.5 g L^{-1}. Low phosphorus bioavailability in these lakes may be due to binding with the large dissolved organic carbon pools, as was suggested for Saskatchewan saline lakes (Waiser and Robarts 1995). At conductivities > 3 mS cm^{-1}, iron limitation emerges as the key factor controlling phytoplankton standing crops and Chl *a* concentrations tend to be very low (0.5 to 20 µg L^{-1}), even at extremely high concentrations of available phosphorus (> 1 mg L^{-1}). Hammer

(1986a) suggested that lakes with TDS between 0.5 and 3 g L^{-1} should be classified as subsaline and lakes with TDS above 3 g L^{-1} as saline; my observations in Alberta lakes suggest that this classification has some biological significance.

(4) *Influence of zooplankton.* The effects of grazing and zooplankton waste excretion on Alberta saline lake phytoplankton need to be explored further. Zooplankton grazing was postulated to be an important factor in maintaining low phytoplankton standing crops in saline Redberry Lake, Saskatchewan (Evans et al. in press). Zooplankton biomasses in the more saline (> 3 mS cm^{-1}) lakes were consistently greater than phytoplankton biomasses, as was the case in Redberry Lake, and likely had a similar effect on the phytoplankton standing crop. The presence of cyanophytes in the zooplankton gut suggest that members of this phylum, often considered to be inedible, are at least being ingested along with other taxa, further study is needed to determine if zooplankton have any influence on the phytoplankton species compositions of these lakes.

4.2: References

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Appendix A:

Conductivity, nutrient, ion and chlorophyll *a* data for the 12-year study.

Table A1: Birch Lake conductivity, pH, ion concentrations, chlorophyll *a* (Chl *a*), total (TP), dissolved (TDP) and soluble reactive (SRP) phosphorus for the 1982-1994 study period. Blanks indicate no data.

Sampling Date	Conductivity (uS cm^{-1})	Phosphorus (ug L^{-1})				Chl *a*	Ion concentration (meq L^{-1})								
		TP	TDP	SRP	pH	(ug L^{-1})	Na^+	K^+	Ca^{2+}	Mg^{2+}	$SO_4^{=}$	Cl^-	HCO_3^-	$CO_3^{=}$	Alkalinity
8/1/82	16940	21920			8.70	7.0					67				86.6
5/16/83	19300	10642	10268		9.47	8.7	220	2.94	0.69	4.49		8.67	40.4	65.3	105.7
6/6/83	20240	13630	13448		9.62	9.4	232	3.05	0.99	3.93	140	8.46	40.5	70.7	111.2
6/23/83	18150	13228	13236		9.61	11.7	229	3.39	0.79	6.24	141	9.51	37.8	72.4	110.2
7/17/83	17530	13447	13210		9.50	7.0	227	4.25	0.83	5.37	136	9.21	37.7	67.3	105.0
8/8/83	18040	13199	12990		9.62	62.0	222	3.46	0.76	8.94	138	8.99	38.8	75.3	114.1
8/26/83	17930	14163	14060		9.48	2.8	236	3.43	1.36	3.46	138	9.08	38.4	86.7	125.1
8/1/86											130	7.90			
3/31/87						7.6					163	10.50			
5/15/87	17070	12464	11756		9.54	6.8	252	2.79	0.20	2.13	123	8.70	35.1	65.6	100.7
6/11/87	18640	13280			9.50	27.3					129	8.80	38.1	68.0	106.1
7/15/87	20250	14306			9.58	13.5					135	8.40	23.0	40.5	63.5
8/13/87	21270	13586			9.61	6.0	154	3.15	0.28	2.32	139	8.30	21.7	43.9	65.6
5/25/92	24240	17560			9.48	9.2							51.2	61.9	113.1
6/8/92	23900	15800			9.53	8.4							38.7	60.5	99.2
6/29/92	24750	19700			9.49	5.8							68.1	72.5	140.6
7/20/92	28810	19640			9.53	1.4	350	7.19	0.39	3.63			66.4	74.0	140.4
8/10/92	28810	22920			9.53	2.4	295	5.61	0.99	7.54			66.7	75.9	142.5
8/24/93	32320	22420	23000		9.59	21.7					252	16.93			
5/3/94	25700	15010	16470	16840		0.7	319	4.24	0.26	2.49	216	13.48			
5/25/94						4.3									
6/20/94	30800	25550	25200	24560	9.62	1.8									
7/7/94	30900	22100	19900	20500	9.66	1.3	480	6.01	0.16	4.37	282	18.36	71.5	101.7	173.2
7/19/94	30700	26380	25850	25370	9.64	13.2							73.1	101.9	175.0
8/2/94	30500	25900	24280	24430	9.64	3.3							69.3	111.3	180.6
8/15/94	28900	28260	25550	24950	9.62	1.4	519	8.32	0.15	3.79	282	16.80	119.5	160.0	279.5
9/13/94	29700	25930	26800	25960	9.62	2.1	490	6.03	0.16	4.59	294	17.93	114.7	154.9	269.6

Table A2: Camp Lake conductivity, pH, ion concentrations, chlorophyll *a* (Chl *a*), total (TP), dissolved (TDP) and soluble reactive (SRP) phosphorus for the 1982-1994 study period. Blanks indicate no data.

Sampling Date	Conductivity (uS cm^{-1})	Phosphorus (ug L^{-1})				Chl *a*	Ion concentration (meq L^{-1})								
		TP	TDP	SRP	pH	(ug L^{-1})	Na^+	K^+	Ca^{2+}	Mg^{2+}	$SO_4^=$	Cl^-	HCO_3^-	$CO_3^=$	Alkalinity
8/1/82	1694	93			8.7	25.9									16.2
5/16/83	1791	157	38		9.11	49.51	12.4	0.69	0.70	6.72	4.03	0.32	9.6	6.5	16.2
6/6/83	1917	143	32		9.31	36.12	13.7	0.92	0.86	6.49	4.39	0.34	9.4	7.2	16.6
6/23/83	1837	191	99		9.32	63.28	12.8	0.89	0.77	7.57	7.78	0.23	9.8	7.3	17.1
7/17/83	1809	185	49		9.2	40.09	13.5	1.11	0.75	6.93	4.45	0.34	9.4	8.0	17.4
8/8/83	1859	204	58		9.24	2.4	13.6	0.92	0.64	8.17	4.85	0.34	9.6	6.4	16.0
8/26/83	1760	220	53		9.16	85.97	14.1	0.93	1.01	8.82	4.40	0.32	8.7	9.3	18.0
8/1/86											4.40	0.30			
3/31/87											5.80	0.50			
5/14/87	1810	144	33		8.97	33.1	13.1	0.84	0.62	6.67	4.00	0.30	11.0	5.2	16.2
6/11/87	1860	136			9.09	23.1					4.40	0.30	11.4	6.4	17.8
7/15/87	1820	190			9.26	43.9					4.80	0.30	5.8	5.2	11.0
8/13/87	2040	185			8.96	70.5	9.8	1.00	0.43	7.25	4.20	0.30	6.6	3.7	10.3
5/31/90	1386	140	62		9.09	49.7			0.58	7.94					
6/25/90	1562	161	12		9.17	72.4									
7/17/90	1408	200	43		9.23	93.5									
8/8/90	1336	167	49		9.14	53.3									
5/15/91	2050	188	31		9.07	46.38	15.6	0.86	0.47	6.75			15.0	3.8	18.8
6/4/91	2080	189	21		9.14	33.45							13.9	4.2	18.1
6/26/91	2190	159	26		9.1	35.9	15.2	0.93	0.48	6.84			13.6	4.9	18.5
7/16/91	2100	180	27		9.26	50.52	15.9	0.94	0.45	7.81			14.6	6.1	20.7
7/30/91	2320	200	29		9.29	50.24	18.1	1.03	0.37	7.55			14.2	6.6	20.8
8/20/91	2340	162	30		9.26	34.13	17.0	1.04	0.29	7.48			14.6	6.1	20.7
9/17/91						59.8									
5/25/92	2033	181			9.01	32.89							15.4	4.3	19.7
6/8/92	2339	164			9.07	33.53							13.4	4.9	18.3
6/29/92	2178	154			9.11	34.86							15.2	5.0	20.2
7/20/92	2186	157			9.19	47.56	18.2	1.62	0.29	7.99			15.6	4.8	20.4
8/10/92	2203	203			9.23	65.26	13.3	1.01	0.21	9.17			15.8	6.1	21.9

Table A2 continued

Sampling Date	Conductivity (uS cm^{-1})	Phosphorus (ug L^{-1})			pH	Chl *a* (ug L^{-1})	Ion concentration (meq L^{-1})								
		TP	TDP	SRP			Na^+	K^+	Ca^{2+}	Mg^{2+}	$SO_4^{=}$	Cl^-	HCO_3^-	$CO_3^{=}$	Alkalinity
8/24/93															
5/3/94	2420	140	18	2		52.04	17.0	1.06	0.34	12.4	0.41	5.31			
6/20/94	2070	177	68	58		35.18									
7/7/94	2100	143	21	5		41.14	19.0	1.16	0.30	7.51	0.45	5.57	13.1	7.0	20.0
7/19/94	1810	152	16	16		37.39							12.3	7.1	19.4
8/2/94	2100	154	33	15		25.62							13.9	6.7	20.6
8/15/94	1880	114	25			26.06	18.5	1.11	0.26	7.88	0.43	5.43	16.7	19.1	35.8
9/13/94	2060	170	34	18		38.28	20.0	1.17	0.32	9.56	0.44	6.26	21.7	10.0	31.7

Table A3: Fluevog Lake conductivity, pH, ion concentrations, chlorophyll *a* (Chl *a*), total (TP), dissolved (TDP) and soluble reactive (SRP) phosphorus for the 1982-1994 study period. Blanks indicate no data.

Sampling Date	Conductivity (uS cm^{-1})	Phosphorus (ug L^{-1})				Chl *a*	Ion concentration (meq L^{-1})								
		TP	TDP	SRP	pH	(ug L^{-1})	Na^+	K^+	Ca^{2+}	Mg^{2+}	$SO_4^{=}$	Cl^-	HCO_3^-	$CO_3^{=}$	Alkalinity
8/1/82	8800	2242			9.20	2.8					41.3				38.7
5/17/83	9090	2131	2073		9.23	3.3	107	1.30	1.02	3.93	52.2	3.73	23.8	17.5	41.3
6/6/83	9500	2230	2112		9.28	1.5	102	1.06	1.30	3.75	43.7	3.99	24.9	18.7	43.6
6/20/83	9430	2165	2006		9.20	2.7									41.6
6/24/83	9250	2162	2111		9.28	1.6	93	1.62	1.21	5.18	56.3	3.96	25.0	16.7	41.7
7/6/93	9020	2118	1969		9.16	4.7									43.6
7/18/83	8880	2136	2109		9.20	5.2	94	2.04	1.18	4.56	57.1	4.06	24.2	17.7	41.9
7/19/83	8800	2103	2011		9.15	3.6									41.6
8/9/83	9460	2203	2121		9.28	9.7	103	1.77	0.96	6.77	60.4	4.17	24.4	18.4	42.8
8/11/83	9400	2171	2064		9.19	6.5									42.8
8/28/83	9620	2336	2266		9.19	2.6	103	1.78	2.05	4.62	60.7	4.16	23.2	23.9	47.1
10/1/83	9740	2261	2150												
2/13/84	12100														
3/18/84	12650														
4/9/84	11000														
4/20/84	11550														
5/7/84	11000	2118	2025			4.5									
5/16/84	10450	2149	2015		9.17	2.4									41.2
5/30/84	8800	2331	2116		9.18	3.6									42.4
6/11/84	10450	2248	2091			0.9									
6/20/84	10450	2192	1996		9.21	1.1									41.2
7/5/84	9900	2260	2111		9.31	3.8									41.8
7/18/84	9900	2366	2215			4.0									
7/25/84	10450	2351	2157		9.15	5.1									43.2
8/9/84	11000	2447	2187		9.18	5.5									46.2
8/22/84	9900	2550	2355		9.11	2.2									45.8
8/29/84	11000	2550	2295			2.3									
8/15/86											61.8	4.6			
3/31/87						2.3					85.4	5.8			

Table A3 continued

Sampling Date	Conductivity (uS cm^{-1})	Phosphorus (ug L^{-1})			pH	Chl *a* (ug L^{-1})	Ion concentration (meq L^{-1})								
		TP	TDP	SRP			Na^+	K^+	Ca^{2+}	Mg^{2+}	$SO_4^{=}$	Cl^-	HCO_3^-	$CO_3^{=}$	Alkalinity
5/17/87	8680	2218	1980		9.19	8.8	101	1.34	0.44	3.30	48.0	3.5	29.7	10.6	40.3
6/11/87	9550	2298			9.16	2.6					57.8	5.4	32.7	11.2	43.9
7/15/87	9890	2441			9.47	3.2					60.2	3.9	17.9	9.4	27.3
8/13/87	10030	2220			9.02	3.5	74	1.45	0.44	3.41	58.4	4.2	19.9	9.0	28.9
5/31/90	13860	1200	1124		9.22	2.1			0.44	4.40					
6/25/90	13550	1264	1264		9.29	6.8									
7/17/90	15180	1412	1293		9.35	3.9									
8/8/90	16180	1352	1329		9.29	3.3									
5/15/91	13700	1580	1470		9.41	7.2	124	1.58	0.37	3.63			30.4	20.3	50.7
6/4/91	11220	1840	1750		9.39	1.0							33.1	20.3	53.5
6/26/91	14520	1830	1660		9.38	2.1	123	1.54	0.20	3.59			27.0	21.3	48.3
7/16/91	11110	1760	1630		9.44	4.0	129	1.66	0.12	3.60			33.2	23.6	56.8
7/30/91	15180	1787	1640		9.48	5.7	137	1.56	0.06	3.69			32.2	26.2	58.5
8/20/91	15950	1810	1720		9.42	4.7	140	1.80	0.07	3.87			45.6	22.5	68.2
9/9/91		1860	2150		9.38	2.9									
9/17/91						3.1									
5/27/92	11690	2058			9.28	42.5							36.0	19.5	55.5
6/9/92	12034	2089			9.29	1.8							39.6	20.8	60.4
6/30/92	12542	2360			9.25	3.4							43.4	22.4	65.8
7/21/92	13390	2396			9.30	6.4	156	3.63	0.36	4.53			40.1	22.7	62.8
8/11/92	13390	2568			9.29	10.1	153	2.37	0.39	5.31			41.8	24.9	66.6
8/2/94	11920	1752	1509	1300	9.63	6.7	196	3.07	0.42	8.25	139.2	6.37	32.2	35.7	67.9

Table A4: Joseph Lake conductivity, pH, ion concentrations, chlorophyll *a* (Chl *a*), total (TP), dissolved (TDP) and soluble reactive (SRP) phosphorus for the 1982-1994 study period. Blanks indicate no data.

Sampling Date	Conductivity (uS cm^{-1})	Phosphorus (ug L^{-1})			pH	Chl *a* (ug L^{-1})	Ion concentration (meq L^{-1})								
		TP	TDP	SRP			Na^+	K^+	Ca^{2+}	Mg^{2+}	$SO_4^{=}$	Cl^-	HCO_3^-	$CO_3^{=}$	Alkalinity
5/3/83	3025	337	187		9.09	77.9	28.2	1.51	1.19	4.00	12.80	0.84	10.0	7.2	17.2
5/24/83	3170	227	174		9.18	4.3	25.4	1.46	1.08	3.65	13.46	1.37	10.7	7.2	17.9
6/13/83	3170	268	331		9.14	7.5	26.4	1.68	1.35	3.86	14.48	0.95	11.6	6.7	18.3
7/4/93	2920	250	210		9.00	63.8	25.4	1.62	1.23	3.87	12.39	1.13	10.9	4.5	15.4
7/25/83	2880	236	163		8.91	32.7	24.3	2.05	1.22	3.79	12.23	0.88	11.4	3.2	14.6
8/15/83	3010	457	233		8.95	60.1	25.6	1.56	1.48	4.31	13.09	0.92	11.4	4.1	15.5
8/15/86											12.60	0.80			
3/29/87						24.0					17.40	1.30			
5/16/87	2940	797	582		9.08	76.4	21.3	1.25	0.91	3.70	10.40	0.80	12.0	4.2	16.2
6/12/87	2830	782			9.10	30.9					11.60	0.90	13.0	3.8	16.9
7/16/87	3010	1031			9.22	62.4					11.60	0.90	7.7	2.8	10.5
8/14/87	2870	822			9.24	115.0	21.3	1.25	1.06	3.73	11.40	0.90	7.2	3.3	10.5
6/6/90	2610	498	468		9.02	9.7			0.93	4.61					
6/26/90	2210	321	243												
7/19/90	2510	568	519			94.4									
8/8/90	2590	559	466			36.8									
5/17/91	3250	297	234		8.93	9.8	24.8	1.38	0.88	3.98			14.8	2.6	17.3
6/3/91	2980	518	473		8.91	7.2	27.5	1.40	0.88	4.07			15.2	2.5	17.7
6/25/91	3080	564	540		8.98	21.0	26.4	1.47	0.92	4.28			13.1	3.3	16.4
7/15/91	3120	623	524		9.22	35.7	27.9	1.47	0.92	4.24			13.5	4.8	18.4
7/29/91	3070	483	422		8.98	11.5	28.5	1.52	0.96	4.33			15.3	3.8	19.1
8/19/91	3470	658	531		9.02	38.6	29.1	1.57	1.02	4.45			14.1	3.7	17.7
9/18/91						25.2									
5/6/92	3197	449			8.88	22.9	14.0	1.40	0.91	4.17			14.8	2.6	17.5
5/26/92	3254	589			8.88	15.1							15.0	2.8	17.7
6/15/92	3077	669			8.84	8.4							16.2	2.2	18.4
7/6/92	3338	979			8.92	17.1							16.0	3.7	19.7
7/14/92	3371	1019			8.90	27.2							15.6	4.0	19.6
7/27/92	3475	1137			8.92	35.3	27.2	1.79	0.96	5.67			16.5	3.2	19.7

Table A4 continued

Sampling Date	Conductivity (uS cm^{-1})	Phosphorus (ug L^{-1})			pH	Chl *a* (ug L^{-1})	Ion concentration (meq L^{-1})								
		TP	TDP	SRP			Na^+	K^+	Ca^{2+}	Mg^{2+}	$SO_4^{=}$	Cl^-	HCO_3^-	$CO_3^{=}$	Alkalinity
8/17/92	3559	1122			9.00	45.8	10.5	1.87	1.00	5.72			15.8	3.7	19.5
8/26/93	3210	1382	1445	1371		19.5									
5/3/94	3860	1240	1120	1140		9.5	33.6	1.77	0.67	2.83	16.79	1.37			
6/20/94	3580	1530	1510	1430	9.12	6.5									
7/7/94	3510	1570	1485	1364	9.15	2.1	37.7	2.00	0.72	8.83	18.38	1.42	9.2	15.1	24.3
7/21/94	3540	1510	1510	1400	9.21	3.8							20.4	3.1	23.5
8/2/94	3450	1690	1640	1400	9.20	1.9							16.9	5.4	22.2
8/15/94	3240	1777	1627	1496	9.15	15.4	37.9	2.14	0.92	5.00	18.19	1.40	0.8	44.7	45.5
9/13/94	3290	1456	1368	1300	9.08	4.6	37.2	1.89	0.93	8.96	17.94	1.44	24.0	7.5	31.5

Table A5: Peninsula Lake conductivity, pH, ion concentrations, chlorophyll *a* (Chl *a*), total (TP), dissolved (TDP) and soluble reactive (SRP) phosphorus for the 1982-1994 study period. Blanks indicate no data.

Sampling Date	Conductivity (uS cm^{-1})	Phosphorus (ug L^{-1})				Chl *a*	Ion concentration (meq L^{-1})								
		TP	TDP	SRP	pH	(ug L^{-1})	Na^+	K^+	Ca^{2+}	Mg^{2+}	$SO_4^{=}$	Cl^-	HCO_3^-	$CO_3^{=}$	Alkalinity
8/1/82	12870	3573			9.20	2.4					75				42.1
5/11/83	12380	3323	3233		9.19	10.0									43.0
5/17/83	12870	3422	3372		9.25	8.9	160	2.35	1.15	6.80		4.78	24.1	20.8	44.9
5/19/83	12210	3592	3316		9.25	11.0									42.8
6/7/83	13150	3625	3405		9.23	6.8									44.4
6/21/83	13200	3399	3247		9.25	2.0									43.7
6/24/83	12320	3384	3349		9.38	1.9	140	2.64	1.28	9.10	100	4.96	23.3	23.1	46.4
7/7/93	12650	3420	3220		9.20	2.3									43.4
7/18/83	12210	3495	3404		9.20	4.8	139	3.43	1.28	8.44	99	5.04	24.7	20.5	45.2
7/20/83	12930	3438	3301		9.21	4.3									43.4
8/9/83	12600	3509	3447		9.29	2.1	145	2.77	1.12	11.79	102	5.15	24.0	22.0	46.0
8/12/83	13200	3385	3270		9.22	3.6									44.0
8/27/83	12600	3662	3528		9.25	17.9	148	2.77	2.23	7.99	102	5.19	20.4	29.3	41.8
10/1/83	12760	3612	3497		9.23	8.2									45.0
1/17/84	13750														
2/13/84	15290														
3/18/84	17600														
4/20/84	12100														
5/7/84	15400														
5/15/84	15290	3439	3324		9.27	2.6									43.8
5/29/84	13200	3649	3443		9.22	2.4									44.6
6/11/84	14850	3553	3378			0.5									
6/19/84	14300	3512	3271		9.26	1.2									43.0
7/4/84	14300	3679	3223		9.12	3.3									44.3
7/16/84	14300	3756	3609			4.3									
7/24/84	14300	3638	3544		9.25	84.5									45.4
8/8/84	15400	3867	3639		9.16	7.3									51.0
8/21/84	15400	4034	3883		9.13	3.7									48.6
8/27/84	15400	3785	3673			3.8									

Table A5 continued

Sampling Date	Conductivity (uS cm^{-1})	Phosphorus (ug L^{-1})			pH	Chl *a* (ug L^{-1})	Ion concentration (meq L^{-1})								
		TP	TDP	SRP			Na^+	K^+	Ca^{2+}	Mg^{2+}	$SO_4^{=}$	Cl^-	HCO_3^-	$CO_3^{=}$	Alkalinity
8/15/86											101	4.8			
3/31/87						0.5					127	6.6			
5/17/87	11730	2068	1980		9.29	5.7	118	2.30	0.38	5.77	87	4.8	26.8	13.2	39.9
6/10/87	11660	2298			9.28	9.1					93	5.0	28.4	13.8	42.1
7/15/87	12970	2441			9.51	3.0					97	5.1	16.5	10.1	26.6
8/13/87	13220	2220			9.34	4.1	105	2.40	0.49	6.12	97	5.1	15.5	9.6	25.1
5/31/90	16810	1414	1302		9.23	3.9			0.73	7.80					
6/25/90	16090	2025	2010		9.28	1.5									
7/17/90	16780	1902	1761		9.33	4.4									
8/8/90	17050	1872	1740		9.27	2.9									
5/15/91	19250	3382	3342		9.30	2.4	163	2.50	0.44	6.61			31.2	17.2	48.4
6/4/91	14190	3616	3620		9.30	1.5							32.4	17.0	49.4
6/26/91	21160	4123	3975		9.25	3.0	165	2.66	0.25	6.64			30.6	19.8	50.4
7/16/91	17570		3663		9.38	6.2	159	2.51	0.20	7.00			32.1	20.3	52.4
7/30/91	16740	3957	3345		9.40	10.0	170	2.52	0.11	7.26			31.8	21.9	53.7
8/20/91	18650	3494	3414		9.40	3.0	168	2.80	0.15	7.22			30.2	22.2	52.4
9/17/91						2.5									
5/27/92	14067	3321			9.34	15.1							28.5	20.9	49.5
6/9/92	14208	4062			9.33	11.5							20.2	20.3	40.5
6/30/92	14237	3826			9.31	1.3							34.7	20.8	55.5
7/21/92	14915	4097			9.32	1.7	188	4.72	0.52	7.59			34.1	21.9	56.0
8/11/92	15085	4192			9.29	2.1	174	3.43	0.55	9.81			35.2	20.9	56.1
8/2/94	14200	3760	3636	3590	9.54	5.3	180	2.11	0.24	6.88	92	6.20	28.7	32.0	60.6

Table A6: Wappa Lake conductivity, pH, ion concentrations, chlorophyll *a* (Chl *a*), total (TP), dissolved (TDP) and soluble reactive (SRP) phosphorus for the 1982-1994 study period. Blanks indicate no data.

Sampling Date	Conductivity (uS cm^{-1})	Phosphorus (ug L^{-1})				Chl *a*	Ion concentration (meq L^{-1})								
		TP	TDP	SRP	pH	(ug L^{-1})	Na^+	K^+	Ca^{2+}	Mg^{2+}	$SO_4^{=}$	Cl^-	HCO_3^-	$CO_3^{=}$	Alkalinity
8/1/82	2270	956			8.60	26.6					7.60				15.1
5/16/83	2890	1182	1184		8.93	9.6	25.5	0.42	1.26	2.03	13.42	0.48	10.7	5.1	15.8
6/6/83	3010	1312	1132		9.06	9.7	26.4	0.66	1.50	2.02	13.55	0.60	10.4	6.5	16.9
6/23/83	2920	1372	1203		9.02	4.9	28.0	0.70	1.50	2.60	15.33	0.28	11.4	4.3	15.7
7/17/83	2870	1694	1958		8.96	17.3	26.2	0.82	1.38	2.03	13.19	0.54	10.4	3.7	14.1
8/8/83	2780	1303	1211		9.02	38.4	25.1	0.67	1.33	2.68	13.47	0.54	10.6	4.4	15.0
8/26/83	2920	1347	1264		9.10	80.6	27.1	0.65	2.38	2.32	13.52	0.53	10.6	6.0	16.6
8/15/86											12.60	0.50			
3/31/87						1.3					22.60	1.00			
5/15/87	2810	1160	1039		9.09	13.5	23.9	0.58	1.06	1.97	11.80	0.50	13.6	2.4	16.0
6/11/87	2940	1309			9.03	31.4					12.80	0.60	15.2	2.6	17.8
7/15/87	3050	1208			9.17	398.0					13.60	0.60	7.7	3.2	10.9
8/13/87	3330	1318			9.27	18.2	22.8	0.70	1.00	2.10	13.40	0.70	8.7	3.0	11.7
5/31/90	2010	999	906		9.02	2.1			0.80	2.20					
6/25/90	2410	1089	968		9.50	3.8									
7/17/90	2580	1070	1055		9.10	10.4									
8/8/90	2860	956	894		9.00	4.3									
5/15/91	3690	1397	1308		9.03	7.6	33.1	0.61	0.73	2.11			16.7	3.6	20.3
6/4/91	3450	1547	1420		9.03	9.1							16.0	3.3	19.3
6/26/91	3150	1624	1468		8.99	14.4	36.1	0.72	0.72	2.04			15.9	3.8	19.8
7/16/91	3900	1624	999		9.28	87.6	37.0	0.66	0.70	2.13			16.0	6.0	22.0
7/30/91	3850	1819	1645		9.14	3.8	38.6	0.77	0.75	2.28			17.1	5.4	22.5
8/20/91	4240	2083	1574		9.16	38.5	38.5	0.78	0.96	2.47			17.5	5.3	22.8
9/17/91						19.7									
5/25/92	3898	2206			9.04	4.0							17.9	5.2	23.1
6/8/92	4051	1889			9.11	5.4							17.4	5.1	22.5
6/29/92	4220	1975			9.23	67.9							17.9	7.4	25.3
7/20/92	4407	2034			9.26	30.4	94.8	1.75	0.86	3.13			18.6	7.2	25.8
8/10/92	4407	2044			9.24	25.3	40.2	0.87	0.79	3.49			19.0	8.0	26.9

Table A6 continued

Sampling Date	Conductivity (uS cm^{-1})	Phosphorus (ug L^{-1}) TP	TDP	SRP	pH	Chl *a* (ug L^{-1})	Ion concentration (meq L^{-1}) Na^+	K^+	Ca^{2+}	Mg^{2+}	$SO_4^{=}$	Cl^-	HCO_3^-	$CO_3^{=}$	Alkalinity
4/29/93						3.3									
5/10/93		923	770	897		6.9							20.2	6.7	26.8
5/17/93		2164	1988	1836		1.8							19.0	6.2	25.1
5/25/93		2521	2037	1783		1.0									
6/4/93		2172	1943	396	9.49	2.0									
6/14/93		1779	2130	2214	9.21	4.4									
6/22/93		2415	2084	2387	9.23	8.1					22.90	1.07	19.9	6.8	26.7
6/28/93		2222	2047	1907		11.8					21.90	2.08	20.7	7.1	27.8
7/5/93		2138	2081	2053	9.30	2.7									
7/14/93		3555	1984	1926		6.0					25.60	0.44			
7/21/93		4323	2203	2238		3.7									
7/26/93		2424	2216	2176		4.4									
7/29/93						3.2						1.32			
8/3/93		2181	2079	2130		5.4					23.50	0.76			
8/9/93		3184	2961	2983		1.8									
8/16/93		2343	2710	2750	9.26	4.6									
8/24/93					8.99	7.3					28.60	1.14			
8/30/93						4.4									
10/3/93															
5/3/94	4870	1780	1740	1820		1.4	41.9	1.53	0.31	0.16	22.60	0.88			
5/25/94						1.1									
6/20/94	4630	2200	2120	2091	9.25	3.4									
7/7/94	4560	2160	2020	1900	9.30	3.5	52.7	0.88	0.50	1.84	22.10	0.92	16.3	12.7	29.0
7/19/94	4420	2200	2170	2100	9.28	5.2							17.9	9.5	27.4
8/2/94	4320	2330	2360	2318	9.30	0.9							20.4	8.1	28.5
8/15/94	3780	2360	2075	2030	9.62	1.4	48.8	1.80	0.35	2.72	19.80	0.89	17.3	24.4	41.7
9/13/94	4080	2220	2160	2060	9.26	1.6	49.4	0.84	0.62	2.70	21.90	0.97	28.7	11.7	40.4

Table A7: Whites Lake conductivity, pH, ion concentrations, chlorophyll *a* (Chl *a*), total (TP), dissolved (TDP) and soluble reactive (SRP) phosphorus for the 1982-1994 study period. Blanks indicate no data.

Sampling Date	Conductivity (uS cm^{-1})	Phosphorus (ug L^{-1})			pH	Chl *a* (ug L^{-1})	Ion concentration (meq L^{-1})								
		TP	TDP	SRP			Na^+	K^+	Ca^{2+}	Mg^{2+}	$SO_4^{=}$	Cl^-	HCO_3^-	$CO_3^{=}$	Alkalinity
8/1/82	4565	5996			8.60	1.4					17				24.2
5/16/83	5500	3902	3660		9.15	6.4	54	0.98	0.87	1.93	31	1.62	15.2	12.4	27.6
6/6/83	5950	4338	4115		9.27	5.8	56	1.18	1.04	1.89	32	1.80	16.8	12.1	28.9
6/23/83	5830	4378	4205		9.24	3.5	59	1.26	1.06	2.55	34	2.08	17.5	11.1	28.6
7/17/83	5360	4114	4039		9.23	15.0	54	1.42	1.02	2.02	30	1.81	16.1	9.3	25.4
8/8/83	5360	3958	3671		9.28	8.4	53	1.16	0.95	2.72	30	1.71	15.9	8.9	24.8
8/26/83	5780	4326	4218		9.16	2.0	58	1.26	1.78	2.06	32	1.74	15.2	12.7	27.9
8/15/86											24	1.30			
3/31/87						0.2					38	2.30			
5/15/87	4160	3230	3155		9.08	8.7	42	0.87	0.35	0.72	22	1.30	16.6	4.6	21.2
6/11/87	4450	3606			9.03	19.2					22	1.60	18.6	4.6	23.3
7/15/87	5100	3812			9.17	11.1					24	2.10	11.1	3.2	14.3
8/13/87	5300	3960			9.27	8.5	39	1.06	0.38	0.86	25	1.70	10.6	3.8	14.4
5/31/90	7640	1619	1494		9.11	6.7			0.58	1.65					
6/25/90	7680	1863	1648		9.17	4.7									
7/17/90	7865	2053	1848		9.23	12.1									
8/8/90	7950	1399	1375		9.07	5.5									
5/15/91	6120	4318	4005		9.15	10.0	56	1.05	0.80	1.66			23.8	7.1	30.9
6/4/91	5780	4465	4352		9.16	5.0							21.6	6.7	28.3
6/26/91	6990	5008	4894		8.99	6.8	60	1.09	0.75	1.70			23.5	6.6	30.1
7/16/91	6500	4799	2282		9.22	5.9	63	1.10	0.78	1.74			24.0	8.5	32.5
7/30/91	6720	5425	5090		9.29	15.3	66	1.15	0.68	1.93			23.7	10.0	33.7
8/20/91	7510	5014	4846		9.26	11.0	68	1.24	0.88	1.99			23.4	10.4	33.8
9/17/91						10.9									
5/25/92	5915	5229			9.16	4.5							24.7	9.9	34.6
6/8/92	5915	7267			9.21	1.8							24.6	10.6	35.2
6/29/92	6970	6160			9.22	7.8							27.1	11.0	38.1
7/20/92	7370	6649			9.25	6.2	90	2.83	0.85	2.52			27.9	11.8	39.7
8/10/92	7710	7216			9.30	3.8	72	1.69	0.92	2.57			28.3	13.8	42.1

Table A7 continued

Sampling Date	Conductivity (uS cm^{-1})	Phosphorus (ug L^{-1}) TP	TDP	SRP	pH	Chl *a* (ug L^{-1})	Ion concentration (meq L^{-1}) Na^+	K^+	Ca^{2+}	Mg^{2+}	$SO_4^{=}$	Cl^-	HCO_3^-	$CO_3^{=}$	Alkalinity
4/29/93						5.1									
5/10/93		6076	5993	2150		14.3							35.3	19.8	55.1
5/17/93		7244	5896	5737		4.7							27.8	14.0	41.8
5/25/93		7882	5793	6072		6.9									
6/4/93		7052	6678	6649		3.2									
6/14/93		6607	7027	6492	9.65	3.4									
6/22/93		7495	7135	7135	9.37	5.3					49	2.79	29.0	15.7	44.7
6/28/93		7970	6790	6587	9.38	16.7					50	2.48	28.8	15.2	44.0
7/5/93		7185	6972	6794		3.5									
7/8/93						6.4									
7/14/93		7399	7385	7227	9.43	2.9					56	0.42			
7/21/93		7960	6643	6580		3.2									
7/26/93		7460	7399	7306		3.9									
7/29/93						1.5									
8/3/93		7588	7399	7214		2.2					48	2.26			
8/9/93		8047	8197	8137		2.7									
8/16/93		7212	6904	6838		0.5									
8/24/93						4.4					58	3.08			
8/30/93					9.38	2.1									
10/3/93					9.38										
5/3/94	8810	6570	6460	6570		8.7	91	1.53	0.33	1.97	44	2.72			
5/25/94						4.7									
6/20/94	8310	7450	7340	7220	9.44	2.0									
7/7/94	8170	7370	7430	7300	9.43	1.6	110	1.84	0.52	0.80	50	2.94	25.7	25.5	51.2
7/19/94	8450	8090	7490	7440	9.45	4.8							27.8	20.4	48.2
8/2/94	8770	7990	7590	7560	9.44	0.4							30.8	20.9	51.7
8/15/94	8650	7360	7240	7120	9.44	5.7	109	1.80	0.59	3.78	43	2.88	28.5	41.0	69.5
9/13/94	8220	7810	7700	7680	9.40	2.8	106	1.91	0.56	2.63	53	3.09	41.8	30.3	72.1

Appendix B:

Climate data for the 12-year study.

Data from Environment Canada Atmospheric Environment Monitoring Service.

Table B1: Summary of historical climate information for Ranfurly station. All figures are annual mean averages or monthly averages as indicated. Data from Environment Canada Atmospheric Environment Monitoring Service. Blanks indicate no data.

	Annual average temperatures (°C)						
Year	Maximum	Minimum	Average	Mean Summer	Rainfall (mm)	Snowfall (cm)	Precipitation (mm)
1905	9.1	-4.1	2.6	13.9	342.4	46.6	389.1
1906	8.6	-4.3	2.2	13.8	452.5	200.6	652.9
1907	5.7	-6.6	-0.4	11.3	340.8	96.2	436.9
1908	8	-4.9	1.6	13.5	401.5	180.8	582.3
1909	5.8	-7.3	-0.7	13.8	292.7	161.9	454.6
1910	8.6	-4.7	2	13.2	277.9	75.8	353.4
1911	6.3	-6.6	-0.1	12.6	392.4	91.9	484.1
1912	8.4	-4.7	1.9	13.9	360.4	71.4	431.9
1913	8	-5.4	1.4	13.0	429.9	88.4	518.2
1914	8.2	-5.3	1.5	13.9	477	106.4	583.4
1915	9	-4.4	2.3	13.8	432.9	75.9	508.7
1916	6.6	-6.7	0	12.7	528.1	144.5	672.5
1917	7.3	-7.3	0	14.2	205.1	102.9	307.9
1918	8.9	-5.8	1.6	13.1	297.9	130.8	428.6
1919	7.9	-6.7	0.6	15.1	195.1	152.2	347.4
1920	7.7	-6.2	0.8	14.1	424.3	160.6	584.7
1921	9	-5.8	1.6	14.5	270.2	109.7	379.7
1922	9.1	-6.2	1.5	15.0	238.1	93.3	331.5
1923	10.5	-4.3	3.1	14.7	337.8	121.3	458.9
1924	8.6	-6	1.4	13.7	315.7	255.9	571.6
1925	9.7	-4.1	2.8	15.6	302.3	178.2	480.4
1926	8.9	-4.7	2.2	14.4			
1927	6.9	-7	0	14.1	383	128	511
1928	10.6	-4.5	3.1	14.6	233.1	72.9	306
1929	9.3	-5.2	2.1	14.9	198.4	143.2	341.7
1930	8.9	-3.5	2.7	14.0	429.4	110.3	540.4
1931	10.1	-2.9	3.6	13.8	464.4	114	578.3
1932	7.7	-5.1	1.4	15.1	172	91.3	263.3
1933	6.6	-6.1	0.3	14.8	276.3	238.1	514.3
1934	9.5	-3.9	2.8	14.4			
1935	6.9	-6.1	0.4	13.5			
1936	7.4	-5.8	0.8	16.2			
1937	8.2	-5.5	1.4	14.7	337	97.5	434.5
1938	9.6	-3.5	3.1	14.7	342.9	127	469.9
1939	8.9	-3.8	2.6	14.6	256.4	188.1	444.4
1940	8.3	-4.2	2.1	14.9	270.6	164.1	434.6
1941	9.4	-3.5	3	15.7	166.3	133.1	299.3
1942	8.6	-4.2	2.2	14.2	457.4	164.3	621.6
1943	9	-3.7	2.7	13.5	331	86.7	417.7
1944	9.9	-3.2	3.4	14.6	407.4	111.5	518.9
1945	7.6	-5.6	1	13.9	238.7	120.5	359.2
1946	8.2	-4.7	1.8	13.7	384.2	140	524.3
1947	8	-4.6	1.7	14.0	344.2	98.1	442.3

Table B1 continued

Year	Annual average temperatures (°C)				Rainfall (mm)	Snowfall (cm)	Precipitation (mm)
	Maximum	Minimum	Average	Mean Summer			
1948	8	-5.3	1.4	15.4	187.3	159.5	346.7
1949	8.4	-5.2	1.6	15.0	238.1	96.5	334.7
1950	6	-6.7	-0.3	14.6	211.9	157.9	369.8
1951	4.8	-6.6	-0.9	13.0	362.6	186.4	549
1952	8.2	-3.6	2.3	13.6	435	60	494.9
1953	8.3	-3.2	2.6	13.7	361.8	162.6	524.3
1954	6.4	-3.7	1.4	12.5	404.1	85.5	489.6
1955	5.5	-5.7	0	13.9	310.1	168.5	478.4
1956	6.7	-4.1	1.4	14.8	396.6	130.7	527.3
1957	7.6	-3.9	1.9	14.1	310.9	85.5	396.4
1958	8.5	-3.1	2.7	15.1	282.8	102.6	385.3
1959	7.2	-3.8	1.7	13.0	309.3	126.3	435.5
1960	7.6	-4	1.8	13.8	318.6	101.3	419.8
1961	7.8	-4.3	1.8	15.8	325.8	114.9	440.7
1962	7.6	-4	1.9	13.5		133.5	
1963	8.5	-2.9	2.8	14.5	299.3	129.8	429.1
1964	7.4	-3.8	1.9	14.7	254.3	90.1	344.2
1965	6.1	-5.1	0.5	14.3	343.2	108.7	451.9
1966	6.1	-5.2	0.5	14.0	259.2	86.7	345.9
1967	7.2	-4.5	1.4	14.3	208.1	145.8	353.9
1968	7.4	-3.5	2	13.4	335.1	78.3	413.5
1969	6.8	-4.7	1.1	14.1	214.6	122.4	337
1970	6.3	-4.4	1	15.2	306.7	129.4	436.1
1971	6.7	-4.4	1.2	15.2	259.9	117.9	377.9
1972	5.5	-5	0.3	14.9	296.8	156.8	453.4
1973	6.9	-3.5	1.7	14.6	465.8	174.7	640.3
1974	7.3	-3.4	2	13.4	306.1	111.4	417.5
1975	6.8	-4.4	1.3	13.9	250.3	122.7	373.2
1976	9.4	-2.1	3.7	14.9	312.1	85.2	397.2
1977	8.4	-2.9	2.8	14.2	338.5	84.1	422.6
1978	7.1	-3.7	1.7	14.6	358.6	88.9	447.5
1979	6.7	-4	1.4	14.0	299.8	107.9	407.7
1980	7.9	-3.3	2.3	14.3	316.7	125.8	442.5
1981	10.3	-1.4	4.5	15.7	237.1	76.3	313.4
1982	5.6	-5.8	-0.1	13.7	307.9	144.8	452.7
1983	7.3	-3.4	2	14.4	348.9	89.5	438.4
1984	7.9	-3.2	2.4	14.7	296.2	109.3	405.5
1985	7.1	-3.9	1.7	14.2	316.1	124.9	441
1986	8.4	-2.4	3.1	14.5	261.4	127.2	388.6
1987	10.6	-1.1	4.8	14.8	216.3	93	309.3
1988	9.8	-1.9	4	15.8	414	64.8	478.8
1989	7.9	-3.3	2.3	14.8	412.4	90.2	502.6
1990							
1991	9.5	-2.2	3.7	15.9	297	95.4	392.4
1992	8.8	-2.3	3.2	14.1	229.8	160.8	390.6

Table B2: Annual total precipitation and lake pan evaporation for the five climate monitoring stations in the study area. Data from Environment Canada Atmospheric Environment Monitoring Service. Blanks indicate no data.

Station:	Vegreville Evaporation	Ranfurly Precipitation	Fabyan Precipitation	Viking Precipitation	Cooking Lake Precipitation
Year	(mm)	(mm)	(mm)	(mm)	(mm)
1982	464.8	452.7	487.6		
1983	524.1	438.4	443.4		
1984	533.6	405.5		443.8	
1985		441			
1986		388.6	451.6		493.9
1987	510.1	309.3	395.1		431.9
1988		478.8	382.6		
1989		502.6	514.4		545
1990	630.6		390		520.3
1991		392.4			
1992	647.8	390.6			
1993	528.3	512.6	468.6	451.2	

Appendix C:

Conductivity, nutrient, ion, chlorophyll *a* and nutrient demand data for May-September 1994.

Table C1: Dilution factors used in laboratory analyses.

			Analysis:					
Lake	TP/TDP/SRP	DOC	Na^+	K+	Ca^{2+}	Mg^{2+}	Cl^-	SO_4^{2-}
[illegible]ch	50	25	1001	21	2	10	295	501
Camp	1	10	101	6	2	16	2.5	11
Cooking	1	10	101	6	3	10	5	26
Fluevog	25	25	801	16	3	10	51	295
Joseph	5	10	201	6	2	31	11	51
Miquelon	1	10	201	11	2	31	21	201
Peninsula	25	25	1001	31	3	21	51	295
Thomas	25	10	1001	11	2	10	201	295
Vernon	100	50	4001	51	2	21	501	2001
Wappa	10	10	201	21	2	10	11	51
Whites	25	10	201	21	2	10	21	201

Dilution factors expressed as total mLs after diluting 1 mL sample with DDW.
A dilution factor of 1 indicates that no dilution was performed.

Table C2: Birch Lake conductivity, pH, ion concentrations, chlorophyll *a* (Chl *a*), total (TP), dissolved (TDP),and soluble reactive (SRP) phosphorus, total Kjeldahl nitrogen (TKN), ammonia (NH_4^+),and Nitrate+nitrite (NO_3^-).

Sampling Date	Conductivity (mS cm^{-1})	Phosphorus (ug L^{-1})				Chl *a*	Ion concentration (g L^{-1})								Nitrogen (ug L^{-1})		
		TP	TDP	SRP	pH	(ug L^{-1})	Na^+	K^+	Ca^{2+}	Mg^{2+}	$SO_4^{=}$	Cl^-	HCO_3^-	$CO_3^{=}$	NH_4^+	NO_3^-	TN
5/3/94	25.7	15010	16470	16840		0.7	7.337	0.166	0.005	0.030	10.38	13.48			43	103	7850
5/25/94						4.3									23	0	
6/20/94	30.8	25550	25200	24560	9.62	1.8									135		
7/7/94	30.9	22100	19900	20500	9.66	1.3	11.041	0.235	0.003	0.053	13.52	0.65	4.36	3.05	108	31	11040
7/19/94	30.7	26380	25850	25370	9.64	13.2							4.46	3.06	124	2	
8/2/94	30.5	25900	24280	24430	9.64	3.3							4.23	3.34	281	65	
8/15/94	28.9	28260	25550	24950	9.62	1.4	11.942	0.326	0.003	0.046	13.53	0.60	6.79	4.41	243	13	11550
9/13/94	29.7	25930	26800	25960	9.62	2.1	11.265	0.236	0.003	0.056	14.12	0.64	7.00	4.65	222	124	9480

Blank indicates that parameter was not measured in the sample.
"0" indicates that analyte concentration was below the detection limit.

Table C3: Camp Lake conductivity, pH, ion concentrations, chlorophyll *a* (Chl *a*), total (TP), dissolved (TDP),and soluble reactive (SRP) phosphorus, total Kjeldahl nitrogen (TKN), ammonia (NH_4^+),and Nitrate+nitrite (NO_3^-).

Sampling Date	Conductivity (mS cm^{-1})	Phosphorus (ug L^{-1})				Chl *a*	Ion concentration (g L^{-1})								Nitrogen (ug L^{-1})		
		TP	TDP	SRP	pH	(ug L^{-1})	Na^+	K^+	Ca^{2+}	Mg^{2+}	$SO_4^{=}$	Cl^-	HCO_3^-	$CO_3^{=}$	NH_4^+	NO_3^-	TN
5/3/94	25.7	15010	16470	16840		0.7	7.337	0.166	0.005	0.030	10.38	13.48			43	103	7850
5/25/94						4.3									23	0	
6/20/94	30.8	25550	25200	24560	9.62	1.8									135		
7/7/94	30.9	22100	19900	20500	9.66	1.3	11.041	0.235	0.003	0.053	13.52	0.65	4.36	3.05	108	31	11040
7/19/94	30.7	26380	25850	25370	9.64	13.2							4.46	3.06	124	2	
8/2/94	30.5	25900	24280	24430	9.64	3.3							4.23	3.34	281	65	
8/15/94	28.9	28260	25550	24950	9.62	1.4	11.942	0.326	0.003	0.046	13.53	0.60	6.79	4.41	243	13	11550
9/13/94	29.7	25930	26800	25960	9.62	2.1	11.265	0.236	0.003	0.056	14.12	0.64	7.00	4.65	222	124	9480

Blank indicates that parameter was not measured in the sample.
"0" indicates that analyte concentration was below the detection limit.

Table C4: Cooking Lake conductivity, pH, ion concentrations, chlorophyll *a* (Chl *a*), total (TP), dissolved (TDP),and soluble reactive (SRP) phosphorus, total Kjeldahl nitrogen (TKN), ammonia (NH_4^+),and Nitrate+nitrite (NO_3^-).

Sampling Date	Conductivity (mS cm^{-1})	Phosphorus (ug L^{-1})				Chl *a*	Ion concentration (g L^{-1})								Nitrogen (ug L^{-1})		
		TP	TDP	SRP	pH	(ug L^{-1})	Na^+	K^+	Ca^{2+}	Mg^{2+}	$SO_4^{=}$	Cl^-	HCO_3^-	$CO_3^{=}$	NH_4^+	NO_3^-	TN
5/3/94	1.95	389	58	3		92.93	0.320	0.054	0.023	0.041	0.255	0.015			0	13	
6/20/94	1.83	425	90	39	9.38	59.17									3	3	
7/7/94	1.90	404	69	5	9.13	78.75	0.369	0.063	0.019	0.073	0.268	0.016	0.25	0.23	8	39	12650
7/21/94	1.83	448	52	10	9.14	77.48							0.68	0.04	0	38	
8/2/94	1.76	384	60	9	9.39	50.15							0.51	0.09	145	16	
8/15/94	1.81	505	56	5	9.31	106.6	0.368	0.062	0.018	0.069	0.261	0.015	0.37	0.58	0	11	13000
9/13/94	1.71	440	36	11	9.45	94.63	0.317	0.061	0.018	0.099	0.301	0.016	0.66	0.16	0	11	11340

Blank indicates that parameter was not measured in the sample.
"0" indicates that analyte concentration was below the detection limit.

Table C5: Joseph Lake conductivity, pH, ion concentrations, chlorophyll *a* (Chl *a*), total (TP), dissolved (TDP),and soluble reactive (SRP) phosphorus, total Kjeldahl nitrogen (TKN), ammonia (NH_4^+),and Nitrate+nitrite (NO_3^-).

Sampling Date	Conductivity (mS cm^{-1})	Phosphorus (ug L^{-1})				Chl *a*	Ion concentration (g L^{-1})								Nitrogen (ug L^{-1})		
		TP	TDP	SRP	pH	(ug L^{-1})	Na^+	K^+	Ca^{2+}	Mg^{2+}	$SO_4^{=}$	Cl^-	HCO_3^-	$CO_3^{=}$	NH_4^+	NO_3^-	TN
5/3/94	3.86	1240	1120	1140		9.5	0.772	0.069	0.013	0.034	0.807	0.048			37	20	5900
6/20/94	3.58	1530	1510	1430	9.12	6.5									121	46	
7/7/94	3.51	1570	1485	1364	9.15	2.1	0.866	0.078	0.014	0.107	0.883	0.050	0.56	0.45	13	64	8100
7/21/94	3.54	1510	1510	1400	9.21	3.8							1.24	0.09	118	53	
8/2/94	3.45	1690	1640	1400	9.20	1.9							1.03	0.16	386	97	
8/15/94	3.24	1777	1627	1496	9.15	15.4	0.870	0.083	0.018	0.061	0.874	0.049	0.81	0.78	202	155	7800
9/13/94	3.29	1456	1368	1300	9.08	4.6	0.856	0.074	0.019	0.109	0.862	0.051	1.46	0.23	54	54	6090

Blank indicates that parameter was not measured in the sample.
"0" indicates that analyte concentration was below the detection limit.

Table C6: Miquelon Lake conductivity, pH, ion concentrations, chlorophyll *a* (Chl *a*), total (TP), dissolved (TDP),and soluble reactive (SRP) phosphorus, total Kjeldahl nitrogen (TKN), ammonia (NH_4^+),and Nitrate+nitrite (NO_3^-).

Sampling Date	Conductivity (mS cm^{-1})	Phosphorus (ug L^{-1})			pH	Chl *a* (ug L^{-1})	Ion concentration (g L^{-1})								Nitrogen (ug L^{-1})		
		TP	TDP	SRP			Na^+	K^+	Ca^{2+}	Mg^{2+}	$SO_4^{=}$	Cl^-	HCO_3^-	$CO_3^{=}$	NH_4^+	NO_3^-	TN
5/3/94	7.76	235	211	172		1.2	1.726	0.111	0.005	0.155	2.54	0.10			32	1	6250
6/20/94	6.92	262	219	236	9.40	1.8									77		
7/7/94	7.16	232	205	148	9.44	1.0	1.837	0.021	0.006	0.239	2.67	0.10	1.09	0.41	3	4	7370
7/21/94	7.57	206	190	128	9.46	1.9							1.25	0.32	0	6	
8/2/94	7.27	222	199	132	9.48	0.6							1.03	0.44	0	4	
8/15/94	6.36	199	163	117	9.47	4.6	1.817	0.117	0.005	0.228	2.69	0.10	1.23	0.87	0	0	6410
9/13/94	7.06	184	157	118	9.46	2.4	1.871	0.119	0.005	0.366	2.81	0.10	1.55	0.66	3	3	5580

Blank indicates that parameter was not measured in the sample.
"0" indicates that analyte concentration was below the detection limit.

Table C7: Thomas Lake conductivity, pH, ion concentrations, chlorophyll *a* (Chl *a*), total (TP), dissolved (TDP),and soluble reactive (SRP) phosphorus, total Kjeldahl nitrogen (TKN), ammonia (NH_4^+),and Nitrate+nitrite (NO_3^-).

Sampling Date	Conductivity (mS cm^{-1})	Phosphorus (ug L^{-1})				Chl *a*	Ion concentration (g L^{-1})								Nitrogen (ug L^{-1})		
		TP	TDP	SRP	pH	(ug L^{-1})	Na^+	K^+	Ca^{2+}	Mg^{2+}	$SO_4^{=}$	Cl^-	HCO_3^-	$CO_3^{=}$	NH_4^+	NO_3^-	TN
5/3/94	18.2	11380	10720	10630		5.4	4.90	0.095	0.010	0.048	7.14	0.56			15	12	5740
6/20/94	17.3	11530	11130	11060	9.42	8.5									20	1	
7/7/94	17.3	10800	9870	11000	9.40	5.3	5.34	0.105	0.013	0.051	7.90	0.60	1.87	0.63	2	24	5890
7/19/94	15.3	10050	9590	9480	9.37	19.8							1.55	0.54	8	4	
8/2/94	16.7	11890	10860	10760	9.40	2.2							1.76	0.66	22	4	
8/15/94	14.6	11860	11590	11270	9.39	7.4	5.37	0.105	0.013	0.064	7.52	0.62	2.68	1.09	0	0	5370
9/13/94	16.9	11860	12040	11700	9.36	8.3	5.56	0.103	0.016	0.081	8.55	0.64			7	18	4720

Blank indicates that parameter was not measured in the sample.
"0" indicates that analyte concentration was below the detection limit.

Table C8: Wappa Lake conductivity, pH, ion concentrations, chlorophyll *a* (Chl *a*), total (TP), dissolved (TDP),and soluble reactive (SRP) phosphorus, total Kjeldahl nitrogen (TKN), ammonia (NH_4^+),and Nitrate+nitrite (NO_3^-).

Sampling Date	Conductivity (mS cm^{-1})	Phosphorus (ug L^{-1})				Chl *a*	Ion concentration (g L^{-1})								Nitrogen (ug L^{-1})		
		TP	TDP	SRP	pH	(ug L^{-1})	Na^+	K^+	Ca^{2+}	Mg^{2+}	$SO_4^{=}$	Cl^-	HCO_3^-	$CO_3^{=}$	NH_4^+	NO_3^-	TN
5/3/94	4.87	1780	1740	1820		1.4	0.96	0.030	0.006	0.002	1.087	0.031			59	4	4000
5/25/94						1.1									45	18	
6/20/94	4.63	2200	2120	2091	9.25	3.4									99		
7/7/94	4.56	2160	2020	1900	9.30	3.5	1.21	0.034	0.010	0.022	1.062	0.033	0.99	0.38	6	16	3820
7/19/94	4.42	2200	2170	2100	9.28	5.2							1.09	0.29	19	7	
8/2/94	4.32	2330	2360	2318	9.30	0.9							1.24	0.24	38	44	
8/15/94	3.78	2360	2075	2030	9.62	1.4	1.12	0.034	0.014	0.033	0.095	0.032	1.06	0.67	38	19	3920
9/13/94	4.08	2220	2160	2060	9.26	1.6	1.14	0.033	0.012	0.033	1.054	0.034	1.75	0.35	34	38	3170

Blank indicates that parameter was not measured in the sample.
"0" indicates that analyte concentration was below the detection limit.

Table C9: Whites Lake conductivity, pH, ion concentrations, chlorophyll *a* (Chl *a*), total (TP), dissolved (TDP),and soluble reactive (SRP) phosphorus, total Kjeldahl nitrogen (TKN), ammonia (NH_4^+),and Nitrate+nitrite (NO_3^-).

Sampling Date	Conductivity (mS cm^{-1})	Phosphorus (ug L^{-1})				Chl *a*	Ion concentration (g L^{-1})								Nitrogen (ug L^{-1})		
		TP	TDP	SRP	pH	(ug L^{-1})	Na^+	K^+	Ca^{2+}	Mg^{2+}	$SO_4^{=}$	Cl^-	HCO_3^-	$CO_3^{=}$	NH_4^+	NO_3^-	TN
5/3/94	8.81	6570	6460	6570		8.7	2.10	0.060	0.007	0.024	2.13	0.10			52	14	5020
5/25/94						4.7									37	1	
6/20/94	8.31	7450	7340	7220	9.44	2.0									174	45	
7/7/94	8.17	7370	7430	7300	9.43	1.6	2.52	0.072	0.011	0.010	2.39	0.10	1.57	0.76	0	65	5020
7/19/94	8.45	8090	7490	7440	9.45	4.8							1.70	0.61	60	49	
8/2/94	8.77	7990	7590	7560	9.44	0.4							1.88	0.63	24	63	
8/15/94	8.65	7360	7240	7120	9.44	5.7	2.49	0.070	0.012	0.046	2.05	0.10	1.78	0.89	11	40	4760
9/13/94	8.22	7810	7700	7680	9.40	2.8	2.44	0.075	0.011	0.032	2.53	0.11	2.55	0.91	38	124	4400

Blank indicates that parameter was not measured in the sample.
"0" indicates that analyte concentration was below the detection limit.

Table C10: Alkaline phosphatase activity (APA) in Camp and Cooking lakes. Activities are in nmoles 3-o methylfluorescein per ug chlorophyll *a* per hour.

Sampling Date	Camp Lake	Cooking Lake
7/19/94	4220	1825
8/2/94	36800	1890
8/15/94	5700	337
9/13/94	2950	184

APA in all other lakes was below detection.

Table C11: 32P-orthophosphate uptake in the saline lakes, measured as % activity on the filter paper. Averages of two runs. Times > 5 minutes are approximate for all lakes except Camp and Cooking.

Sampling Date	Lake	% at 1 minute	% at 5 minutes	% at 30 minutes	% at 3 hours	% at 5 hours
7/19/94	Birch	4	3	2		3
	Camp	55	73	79		
	Thomas	7	7	6	6	
	Wappa	4	5	2		2
	Whites	14	14	2		3
7/21/94	Cooking	56	81	100		
	Joseph	6	6	5	4	
	Miquelon	8	9	7		
8/15/94	Camp	44	88	asymptote reached		
	Cooking	184	100	asymptote reached		

Constistent, low % activity on filter indicates no uptake. Initial activity is probably due to adsorption effects.

Appendix D:

Phytoplankton species composition and biovolumes; May-September 1987, 1991 and 1994.

1987 analyses performed by J. Shamess.
1991 analyses performed by Y. Zhang.
1994 Camp Lake analyses performed by Dr. M. Agbeti.

Table D1: Birch Lake 1987 phytoplankton biovolumes (um^3/mL). Blank indicates zero biovolume.

Taxon	15-May	11-Jun	15-Jul	13-Aug
Unknown chlorophyte filament	18500			
Total Chlorophyta	**18500**	**0**	**0**	**0**
Unknown chrysophyte	52400	156000		52200
Total Chrysophyta	**52400**	**156000**	**0**	**52200**
TOTAL BIOVOLUME	**70900**	**156000**	**0**	**52200**

Table D2: Birch Lake 1994 phytoplankton biovolumes (um^3/mL). Blank indicates zero biovolume.

Taxon	3-May	25-May	20-Jun	7-Jul	19-Jul	2-Aug	15-Aug	13-Sep
Aphanothece sp.	367			355				1260
Coleosphaerum sp.	716	719						
Gomphosphaeria sp.	718	918						
Microcystis sp.						680		
nannoplanktonic	3577	3429	9145	1814	3703	1587	2955	1882
Total other Cyanophyta	**5378**	**5066**	**9145**	**2169**	**3703**	**2267**	**2955**	**3142**
Ankyra sp.					2076	501		
Chorella sp.	58							
Oocystis borgei		130	4686				19085	
Total Chlorophyta	**58**	**130**	**4686**	**0**	**2076**	**501**	**19085**	**0**
Amphora sp.					1171			
Anomoeneis sp.					1331			
Navicula sp.	1386	1276	159		32960	395		
Nitzchia sp.					11641			
Rhopalodia sp.	697	255			3687			
Synedra sp.					1141			
Total Bacillariophyta	**2083**	**1531**	**159**	**0**	**51931**	**395**	**0**	**0**
Rhodomonas minuta			5177	555			3513	3062
Total Cryptophyta	**0**	**0**	**5177**	**555**	**0**	**0**	**3513**	**3062**
Chrysophyte cyst	1726	148	444	12055	22483	30161	3578	6371
Total Chrysophyta	**1726**	**148**	**444**	**12055**	**22483**	**30161**	**3578**	**6371**
TOTAL BIOVOLUME	**9245**	**6875**	**19611**	**14779**	**80193**	**33324**	**29131**	**12575**

Table D3: Camp Lake 1987 phytoplankton biovolumes (um^3/mL). Blank indicates zero biovolume.

Taxon	14-May	11-Jun	15-Jul	13-Aug
Aphanothece clathrata				2.22E+06
Chroococcus limneticus				1.41E+06
Gomphosphaeria lacustris		3.89E+05	1.75E+06	9.35E+05
Lyngbya limnetica	5.67E+06	1.00E+06	2.02E+06	7.80E+05
Merismopedia tenuissima		6.00E+04	1.67E+05	
Merismopedia sp.			1.34E+05	
Oscillatoria tenuis	1.71E+07	5.78E+06	1.21E+07	2.27E+07
Unknown cyanophyte	1.72E+06			
Total other Cyanophyta	**2.45E+07**	**7.23E+06**	**1.62E+07**	**2.80E+07**
Crucigenia quadrata	2.22E+05		2.78E+06	6.95E+04
Eudorina elegans	4.66E+06			
Oocystis sp.			3.08E+04	1.74E+05
Pediastrum sp.		7.35E+05	5.52E+05	2.44E+05
Scenedesmus sp.	8.01E+05		2.64E+04	5.28E+04
Selenastrum sp.	1.00E+05		5.00E+05	
Tetraedron minimum	5.84E+05	1.00E+06	6.26E+05	1.04E+05
Total Chlorophyta	**6.37E+06**	**1.74E+06**	**4.52E+06**	**6.44E+05**
Amphiphora alata	3.34E+07			
Chatoceros elmorei				1.28E+05
Nitzchia sp.	9.59E+05			1.41E+04
Surirella ovata		5.56E+06		
Total Bacillariophyta	**3.44E+07**	**5.56E+06**	**0**	**1.42E+05**
Cryptomonas sp.	1.22E+06			
Total Cryptophyta	**1.22E+06**	**0**	**0**	**0**
Synura uvella				4.45E+05
Total Chrysophyta	**0**	**0**	**0**	**445000**
Euglena sp.		2.78E+05		
Total Euglenophyta	**0**	**2.78E+05**	**0**	**0**
TOTAL BIOVOLUME	**6.64E+07**	**1.48E+07**	**2.07E+07**	**2.93E+07**

Table D4: Camp Lake 1991 phytoplankton biovolumes (um3/mL). Blank indicates zero biovolume.

Taxon	15-May	11-Jun	26-Jun	16-Jul	30-Jul
Aphanocapsa delicatissima	1.02E+05	4.60E+04	4.09E+04	2.28E+05	2.60E+05
Aphanothece clathrata				3.79E+04	3.97E+04
Chroococcus limneticus	8.00E+00	1.98E+04	8.24E+02	1.85E+03	3.25E+03
Dactyloccopsis rhaphidiodes	2.13E+02				
Gomphosphaeria aponica	4.58E+02	1.06E+02		4.58E+02	7.15E+03
Gomphosphaeria lacustris	1.40E+02	2.52E+02			
Lyngbya contorta	5.89E+05	6.13E+06	7.91E+05	7.15E+04	4.46E+05
Lyngbya mucicola					
Merismopedia glaucum	4.45E+04	4.70E+02	6.68E+03	1.21E+06	2.40E+03
Merismopedia minima		6.50E+01	1.06E+02		
Microcystis aeruginosa	5.27E+03	6.20E+03	1.50E+03	3.05E+03	
Microcystis virgidis		1.02E+03	9.89E+02	7.88E+02	2.96E+03
Total other Cyanophyta	**7.42E+05**	**6.20E+06**	**8.42E+05**	**1.56E+06**	**7.62E+05**
Ankistrodesmus sp.				3.20E+01	
Botryococcus braunii	4.88E+02	1.41E+04		3.52E+03	2.94E+03
Characium sp.		7.80E+01	2.94E+02		6.03E+02
Closteropsis sp.					2.45E+02
Cosmarium sp.	4.88E+03		7.33E+03		3.66E+03
Crucigenia rectangularis				2.44E+03	1.15E+03
Dictyosphaeria tetrachotmum	1.14E+04				1.65E+03
Elakatothrix sp.			1.20E+02		6.00E+01
Oocystis pusilla	5.73E+03	5.63E+04	3.91E+02		9.28E+02
Oocysis submarina	5.19E+04				
Pediastrum boryanum	1.54E+05	2.25E+03	5.47E+04	1.22E+04	2.43E+04
Schroederia setigera	9.80E+01	1.17E+03	1.47E+02		
Staurastrum sp.		3.43E+02			1.71E+02
Tetraedron minimum	2.59E+04		6.22E+02	4.98E+02	6.22E+02
Tetrastrum komarekii	6.98E+03	1.17E+02	1.14E+04	1.26E+02	1.80E+04
Total Chlorophyta	**2.61E+05**	**7.44E+04**	**7.51E+04**	**1.88E+04**	**5.43E+04**
Amphora sp.					
Cyclotella sp.	2.20E+03	2.29E+02			1.65E+03
Chaetoceros sp.					
Fragilaria sp.	3.37E+05			7.00E+02	1.35E+05
Navicula sp.			3.50E+02		
Surirella ovata	8.76E+04	5.32E+04		6.57E+03	1.58E+05
Synedra sp.					
Total Bacillariophyta	**4.26E+05**	**5.34E+04**	**3.50E+02**	**7.27E+03**	**2.94E+05**
Cryptomonas sp.	4.33E+05		8.31E+02	831	4.15E+03
Rhodomonas minuta	3.93E+03		1.18E+04		
Total Cryptophyta	**4.37E+05**	**0**	**1.26E+04**	**8.31E+02**	**4.15E+03**
Euglena elastica					
Phacus pyrus					
Total Euglenophyta	**0**	**0**	**0**	**0**	**0**
Gymnodinium sp.					
Total Pyrrophyta	**0**	**0**	**0**	**0**	**0**
TOTAL BIOVOLUME	**1.87E+06**	**6.33E+06**	**9.30E+05**	**1.58E+06**	**1.11E+06**

Table D4: continued

Taxon	20-Aug	17-Sep
Aphanocapsa delicatissima	7.28E+05	9.40E+04
Aphanothece clathrata		
Chroococcus limneticus	1.05E+04	2.43E+04
Dactyloccopsis rhaphidiodes	2.80E+02	
Gomphosphaeria aponica	4.58E+02	
Gomphosphaeria lacustris	7.30E+01	8.40E+01
Lyngbya contorta		1.64E+06
Lyngbya mucicola	2.25E+06	
Merismopedia glaucum	1.85E+04	8.22E+03
Merismopedia minima		1.00E+00
Microcystis aeruginosa	4.13E+03	1.24E+03
Microcystis virgidis		1.22E+03
Total other Cyanophyta	**3.01E+06**	**1.77E+06**
Ankistrodesmus sp.		
Botryococcus braunii	9.38E+03	2.64E+03
Characium sp.		
Closteropsis sp.		
Cosmarium sp.	1.47E+04	4.40E+04
Crucigenia rectangularis		2.01E+03
Dictyosphaeria tetrachotmum	1.98E+03	1.98E+03
Elakatothrix sp.		
Oocystis pusilla	7.04E+03	5.09E+04
Oocysis submarina		
Pediastrum boryanum	9.58E+04	3.65E+04
Schroederia setigera	1.29E+05	8.79E+02
Staurastrum sp.		
Tetraedron minimum	5.98E+03	8.37E+04
Tetrastrum komarekii	7.25E+03	8.05E+03
Total Chlorophyta	**2.71E+05**	**2.31E+05**
Amphora sp.	1.00E+03	1.00E+03
Cyclotella sp.	8.24E+02	7.92E+04
Chaetoceros sp.		2.15E+05
Fragilaria sp.		
Navicula sp.		
Surirella ovata		9.12E+03
Synedra sp.	3.00E+04	4.81E+05
Total Bacillariophyta	**3.19E+04**	**7.85E+05**
Cryptomonas sp.	1.98E+05	4.99E+03
Rhodomonas minuta		
Total Cryptophyta	**1.98E+05**	**4.99E+03**
Euglena elastica	1.36E+04	
Phacus pyrus	2.23E+03	2.23E+03
Total Euglenophyta	**1.58E+04**	**2.23E+03**
Gymnodinium sp.	1.41E+04	
Total Pyrrophyta	**1.41E+04**	**0**
TOTAL BIOVOLUME	**3.51E+06**	**2.79E+06**

Table D5: Camp Lake 1994 phytoplankton biovolumes (um3/mL). Blank indicates zero biovolume.

Taxon	3-May	20-Jun	7-Jul	19-Jul	2-Aug
Total N-fixing Cyanophyta	**0**	**0**	**0**	**0**	**0**
Microcystis sp.	6.00E+04	1.00E+05			
Planktolyngbya circumcreta	1.54E+07	1.09E+08	2.26E+07	1.57E+07	9.38E+06
Oscillatoria agarhdii	6.10E+05	1.92E+06	1.21E+06	3.70E+05	5.50E+05
Pseudanabaena sp.	6.40E+05		6.00E+04	6.00E+04	
Total other Cyanophyta	**1.67E+07**	**1.11E+08**	**2.39E+07**	**1.61E+07**	**9.93E+06**
Cosmarium sp.		4.20E+04	4.80E+05		2.80E+05
Crucigenia quadrata	4.00E+05	1.10E+05	7.20E+04	1.80E+05	6.00E+04
Oocystis sp.		3.10E+04		7.00E+04	
Pediastrum sp.		3.85E+06		6.42E+06	
Quadrigula sp.				1.30E+04	4.00E+04
Scenedesmus sp.	8.00E+04	1.10E+05			
Tetraedron minimum	3.50E+05	6.00E+05	3.50E+05	2.10E+05	8.40E+05
Total Chlorophyta	**8.30E+05**	**4.74E+06**	**9.02E+05**	**6.89E+06**	**1.22E+06**
Nitzchia sp.	7.50E+05	1.10E+05	5.40E+05		
Synedra sp.	1.10E+05	1.20E+05			6.00E+04
Total Bacillariophyta	**8.60E+05**	**2.30E+05**	**5.40E+05**	**0**	**6.00E+04**
Cryptomonas sp.	4.10E+05				2.00E+04
Rhodomonas minuta	1.90E+05			2.10E+04	9.00E+04
Total Cryptophyta	**6.00E+05**	**0**	**0**	**2.10E+04**	**1.10E+05**
TOTAL BIOVOLUME	**1.90E+07**	**1.16E+08**	**2.53E+07**	**2.30E+07**	**1.13E+07**

Table D5: continued

Taxon	15-Aug	13-Sep
Total N-fixing Cyanophyta	**0**	**0**
Microcystis sp.	1.00E+04	3.00E+04
Planktolyngbya circumcreta	1.72E+06	3.35E+06
Oscillatoria agarhdii	2.74E+06	6.09E+07
Pseudanabaena sp.		7.00E+04
Total other Cyanophyta	**4.47E+06**	**6.44E+07**
Cosmarium sp.		
Crucigenia quadrata	4.00E+04	
Oocystis sp.	1.40E+05	
Pediastrum sp.		
Quadrigula sp.		
Scenedesmus sp.		
Tetraedron minimum	7.80E+05	3.50E+05
Total Chlorophyta	**9.60E+05**	**3.50E+05**
Nitzchia sp.	5.00E+04	
Synedra sp.		
Total Bacillariophyta	**5.00E+04**	**0**
Cryptomonas sp.	1.40E+05	
Rhodomonas minuta	1.00E+04	8.00E+04
Total Cryptophyta	**1.50E+05**	**8.00E+04**
TOTAL BIOVOLUME	**5.63E+06**	**6.48E+07**

Table D6: Fluevog Lake 1987 phytoplankton biovolume (um^3/mL). Blank indicates zero biovolume.

Taxon	10-Jul	13-Aug
unidentified cyanophyte		43600
Total other Cyanophyta	**0**	**43600**
Chrysophyte cyst	27900	
Total Chrysophyta	**27900**	
TOTAL BIOVOLUME	**27900**	**43600**

Table D7: Fluevog Lake 1991 phytoplankton biovolume (um^3/mL). Blank indicates zero biovolume.

Taxon	15-May	4-Jun	26-Jun	16-Jul	9/91991	17-Sep
Oscillatoria sp.				14		1916
Total other Cyanophyta	**0**	**0**	**0**	**14**	**0**	**1916**
Ankyra judayi		18696		29297	5064	
Botrycoccus sp.	39	118	666	1926	9462	170
Characium sp.			1496	6076		105
Total Chlorophyta	**39**	**18814**	**2162**	**37299**	**14526**	**275**
Campylodiscus sp.	3589				3589	3589
Frustulina sp.	15044					
Gyrosigma sp.				1600		
Navicula sp.	71682					
Rhopalodia sp.					104288	
Surirella ovata	28695					
unidentified diatom	394477					
Total Bacillariophyta	**513487**	**0**	**0**	**1600**	**107877**	**3589**
Rhodomonas minuta	7697					
Total Cryptophyta	**7697**	**0**	**0**	**0**	**0**	**0**
TOTAL BIOVOLUME	**521223**	**18814**	**2162**	**38913**	**122403**	**5780**

Table D8: Fluevog Lake 1994 phytoplankton biovolume (um^3/mL). Blank indicates zero biovolume.

Taxon	2-Aug
Chroococcus sp.	415071
Microcystis aeruginosa	1878
Oscillatoria sp.	159730
Total other Cyanophyta	**576679**
Botrycoccus sp.	88326
Total Chlorophyta	**88326**
Cymbella turgida	41842
Frustulia rhomboides	1403
Navicula sp.	
Surirella sp.	28695
Total Bacillariophyta	**71940**
Chrysophyte cyst	7697
Total Chrysophyta	**7697**
TOTAL BIOVOLUME	**744642**

Table D9: Joseph Lake 1987 phytoplankton biovolumes (um^3/mL). Blank indicates zero biovolume.

Taxon	16-May	12-Jun	16-Jul	14-Aug
Anabaena flos-aquae		191000	19700	
Anabaena flos-aquae (heterocytes)		8200	1640	
Total N-fixing Cyanophyta	**0**	**199200**	**21340**	**0**
Gomphosphaeria lacustris			39100	23000
Lyngbya limnetica	410000	1960000		177000
Total other Cyanophyta	**410000**	**1960000**	**39100**	**200000**
Chlamydomonas sp.	125000			
Closterium sp.			1870000	6900000
Cosmarium sp.			1360000	882000
Crucigenia quadrata	278000	612000	27800	1580000
Monoraphidium contortum	612000	1480000		148000
Oocystis sp.	55500		3280	6550
Pediastrum duplex	4300000	1.2E+07	57800	138000
Phacus sp.	556000			98400
Selenastrum sp.				50000
unknown cysted chlorophyte	125000			
Total Chlorophyta	**6051500**	**1.4E+07**	**3318880**	**9802950**
Cyclotella sp.	41700	2316		
Navicula sp.	388000	336		
Surirella sp.	3.1E+07		656000	
unknown diatom				673000
Total Bacillariophyta	**3.1E+07**	**2652**	**656000**	**673000**
TOTAL BIOVOLUME	**3.7E+07**	**1.6E+07**	**4035320**	**1.1E+07**

Table D10: Joseph Lake 1991 phytoplankton biovolumes (um^3/mL). Blank indicates zero biovolume.

Taxon	17-May	3-Jun	25-Jun	15-Jul	29-Jul	18-Sep
Aphanizomenon flos-aquae	1547	184480	6482920	1.3E+07	1227050	
A. flos-aquae (heterocytes)	23	11004	146360	83631	206	
Total N-fixing Cyanophyta	**1570**	**195484**	**6629280**	**1.3E+07**	**1.3E+07**	**0**
Chroococcus limneticus					458	
Microcystis flos-aquae	1458	3392	2442	10311	1033090	483520
Total other Cyanophyta	**1458**	**3392**	**2442**	**10311**	**1033548**	**483520**
Ankyra judai		1068	5787		10850	
Botryococcus braunii			486	90		
Characium sp.		19820	5686		12	2982
Closteriopsis sp.						490
Closterium sp.					641	6867
Coelastrum reticulatum						15200
Oocystis sp.					254	
Pediastrum boryanum					3259	35200
Pediastrum duplex	14640	4222		4504	4504	
Sphaerocystis sp.		17420	271	108	488	3516
Total Chlorophyta	**14640**	**42530**	**12230**	**4702**	**20008**	**64255**
Amphiphora sp.		3704				
Cyclotella sp.						4102
Surirella sp.	157860	9970			6647	43200
Total Bacillariophyta	**157860**	**9970**	**0**	**0**	**6647**	**47302**
TOTAL BIOVOLUME	**175528**	**251376**	**6643952**	**1.3E+07**	**1.4E+07**	**595077**

Table D11: Joseph Lake 1994 phytoplankton biovolumes (um^3/mL). Blank indicates zero biovolume.

Taxon	3-May	20-Jun	7-Jul	19-Jul	2-Aug	15-Aug	13-Sep
Aphanizomenon flos-aquae		146360			3E+06	38087	
A. flos-aquae (heterocytes)		4528			159280		
Total N-fixing Cyanophyta	**0**	**150888**	**0**	**0**	**3E+06**	**38087**	**0**
Chroococcus sp.		8456		5109			
Gomphosphaeria sp.		3335	924	21369		8241	
Lyngbya sp.						9281	
Microcystis aeruginosa		569	1356		25298	159119	111556
Total other Cyanophyta	**0**	**12360**	**2280**	**26478**	**25298**	**176641**	**111556**
Ankyra sp.	208		200				
Botryococcus braunii				329304			
Coelastrum sp.		4832	11010				
Cosmarium sp.	6158						7058
Crucigenia quadrata						208	
Oocystis borgei	4598					109265	6248
Pediastrum boryanum			95184	17593		406386	52270
Scenedesmus sp.						208	
Sphaerocystis sp.				1349	11581		
Total Chlorophyta	**10964**	**4832**	**106394**	**348246**	**11581**	**516067**	**65576**
Achnanthes sp.						4863	
Anomoensis sp.						8516	
Cyclotella sp.	57711	2316	5231		1060	16038	1155
Fragilaria sp.							8516
Melosira granulatum	6061				3340	1443	909
Navicula sp.	1802	336					
Nitzchia sp.	3334				2068	399487	52025
Rhoplalodia sp.	2496						
Surirella ovatum	448940						1348
Synedra sp.	304						
Total Bacillariophyta	**520648**	**2652**	**5231**	**0**	**6468**	**430347**	**63953**
Cryptomonas sp.		261756	115962		2615	155506	218980
Total Cryptophyta	**0**	**261756**	**115962**	**0**	**2615**	**155506**	**218980**
TOTAL BIOVOLUME	**10964**	**429836**	**224636**	**374724**	**3E+06**	**886301**	**396112**

Table D12: Miquelon Lake 1994 phytoplankton biovolumes (um^3/mL). Blank indicates zero biovolume.

Miquelon L. Taxon	3-May	20-Jun	7-Jul	19-Jul	2-Aug	15-Aug	13-Sep
Nodularia sp.					231	74028	
Nodularia sp. (heterocytes)						17000	
Total N-fixing Cyanophyta	**0**	**0**	**0**	**0**	**231**	**91028**	**0**
Aphanocapsa sp.		10605					
Gomphosphaeria sp.			757		472		367162
Lyngbya sp.		27					
Microcystis aeruginosa	328		8439			13630	
Total other Cyanophyta	**328**	**10632**	**9196**	**0**	**472**	**13630**	**367162**
Ankistrodesmus sp.	909						
Ankyra sp.		875					
Botryococcus braunii					287142		
Chlorella sp.	2930						
Crucigenia quadrata					294	2084	132
Oocystis borgei					838	11063	838
Scenedesmus sp.							217
Sphaerocystis sp.			3318	46061	6590		
Tetraedron sp.							1238
Total Chlorophyta	**3839**	**875**	**3318**	**46061**	**294864**	**13147**	**2425**
Amphiphora sp.						47290	
Cyclotella sp.	1878		38186		1247	2956	
Melosira granulatum	4525						14872
Navicula sp.	1174		2367	1170	2711	41563	246
Nitzchia sp.	417	62	640	541	131	13716	720
Surirella ovatum			6830		977	49137	
Synedra sp.			87	721	687		1294
Total Bacillariophyta	**7994**	**62**	**48110**	**2432**	**5753**	**154662**	**17132**
Cryptomonas sp.		28910	4269		31822	11449	3018
Rhodomonas minuta	15547	4969	28454	1139	2399	16783	13220
Total Cryptophyta	**15547**	**33879**	**32723**	**1139**	**34221**	**28232**	**16238**
TOTAL BIOVOLUME	**27708**	**45448**	**93347**	**49632**	**335541**	**300699**	**402957**

Table D13: Peninsula Lake 1987 phytoplankton biovolumes (um^3/mL). Blank indicates zero biovolume.

Taxon	17-May	15-Jul	13-Aug
Chroococcus dispersus			89000
Oscillatoria angustissima			28400
Total other Cyanophyta	**0**	**0**	**117400**
Monoraphidium contortum	6080		
Total Chlorophyta	**6080**	**0**	**0**
Rhodomonas minuta	55600		33400
Total Cryptophyta	**55600**	**0**	**33400**
unknown chrysomonad		43600	
Total Chrysophyta	**0**	**43600**	**0**
TOTAL BIOVOLUME	**61680**	**43600**	**150800**

Table D14: Peninsula Lake 1991 phytoplankton biovolumes (um^3/mL). Blank indicates zero biovolume.

Taxon	15-May	4-Jun	26-Jun	16-Jul	17-Sep
Lyngbya mucicola					231
Total other Cyanophyta	**0**	**0**	**0**	**0**	**231**
Ankyra judayi			2894		
Botryococcus braunii		34	786	32910	
Characium sp.		4884	37650		516
Dunalina sp.		248		11260	
Oocystis borgei			136610		13690
Sphaerocystis sp.		147	217		
Total Chlorophyta	**0**	**5313**	**178157**	**44170**	**14206**
Amphiphora sp.					5560
Navicula sp.	6830				
Surirella sp.		3590			3590
Total Bacillariophyta	**6830**	**3590**	**0**	**0**	**9150**
Rhodomonas minuta			73270		7330
Total Cryptophyta	**0**	**0**	**73270**	**0**	**7330**
TOTAL BIOVOLUME	**6830**	**8903**	**251427**	**44170**	**30917**

Table D15 : Peninsula Lake 1994 phytoplankton biovolumes (um^3/mL). Blank indicates zero biovolume

Lake sampled Aug. 2 only. Taxon	**Peninsula**
Nodularia sp.	191
Nodularia sp. (heterocytes)	28
Total N-fixing Cyanophyta	**219**
Chroococcus sp.	17547
Microcystis aeruginosa nannoplanktonic	2045
Oscillatoria sp.	
Spirulina sp.	
Total other Cyanophyta	**19592**
Botrycoccus sp.	186485
Chroococcus sp.	17547
Oocystis borgei	93723
Total Chlorophyta	**297755**
Cymbella turgida	1479
Frustulia rhomboides	6649
Navicula sp.	312
Surirella sp.	34242
Total Bacillariophyta	**42682**
Chrysophyte cyst	
Total Chrysophyta	**0**
TOTAL BIOVOLUME	**360248**

Table D16: Thomas Lake 1994 phytoplankton biovolumes (um^3/mL). Blank indicates zero biovolume.

Taxon	3-May	25-May	7-Jul	19-Jul	2-Aug	15-Aug	13-Sep
Anabaena sp.				8512			
Anabaena sp. (heterocytes)				0			
Nodularia sp.				954			
Nodularia sp.(heterocytes)				32			
Total N-fixing Cyanophyta	**0**	**0**	**0**	**9498**	**0**	**0**	**0**
Lyngbya sp.	713						
Merismopedia minima		41167	623	10034	10187		
Microcystis sp.	1527	1638			3054		
Oscillatoria sp.	501	114					
Pseudanabaena sp.				2464			
Total other Cyanophyta	**2741**	**42919**	**623**	**12498**	**13241**	**0**	**0**
Ankyra sp.		2639	2147	3016			
Crucigenia quadrata		36374	7951	5742	114128	4676	196
Oocystis sp.	1237	8129	26238	1414	14844	10132	1571
Scenedesmus sp.	852						
Tetraedron sp.							113
Total Chlorophyta	**2089**	**47142**	**36336**	**10172**	**128972**	**14808**	**1880**
Cyclotella sp.	91361	795721	11504	718656	191029		
Melosira granulatum	1900						
Navicula sp.	12723	7966		27684	3534		
Nitzchia sp.	2953	19631		22393			
Surirella sp.	3867	159043					3313
Total Bacillariophyta	**112804**	**982361**	**11504**	**768733**	**194563**	**0**	**3313**
Cryptomonas sp.		10603					
Rhodomonas minuta			11875	108385	4156	4156	
Total Cryptophyta	**0**	**10603**	**11875**	**108385**	**4156**	**4156**	**0**
Chrysophyte cyst			442				402
Total Chrysophyta	**0**	**0**	**442**	**0**	**0**	**0**	**402**
Euglena sp.		3308	424		7889		128
Total Euglenophyta	**0**	**3308**	**424**	**0**	**7889**	**0**	**128**
TOTAL BIOVOLUME	**117634**	**1E+06**	**61204**	**909286**	**348821**	**18964**	**5723**

Table D17: Wappa Lake 1987 phytoplankton biovolumes (um^3/mL). Blank indicates zero biovolume.

Taxon	15-May	15-Jul	13-Aug
Aphanizomenon flos-aquae		5.5E+08	1.9E+07
A. flos-aquae (heterocytes)		90600	1310
Total N-fixing Cyanophyta	**0**	**5.5E+08**	**1.9E+07**
Monoraphidium contortum	79500		
Total Chlorophyta	**79500**	**0**	**0**
Cyclotella sp.	132000		
Nitzchia sp.	104000		
Total Bacillariophyta	**236000**	**0**	**0**
Rhodomonas minuta	55600		
Total Cryptophyta	**55600**	**0**	**0**
TOTAL BIOVOLUME	371100	5.5E+08	1.9E+07

Table D18: Wappa Lake 1991 phytoplankton biovolumes (um^3/mL). Blank indicates zero biovolume.

Taxon	15-May	4-Jun	26-Jun	16-Jul	17-Sep
Aphanizomenon flos-aquae		1892	3038400	5335400	42850
A. flos-aquae (heterocytes)		137	97900	156800	1607
Total N-fixing Cyanophyta	**0**	**2029**	**3136300**	**5492200**	**44457**
Microcystis sp.		3662	12120	2950	24250
Total other Cyanophyta	**0**	**3662**	**12120**	**2950**	**24250**
Pediastrum duplex	244	326			
Schroederia setigera		21200			2735
Total Chlorophyta	**244**	**21526**	**0**	**0**	**2735**
Amphora paludosa	100	100			
Fragilaria sp.	52730				
Surirella sp.	933200	93050	6650		
Synedra sp.	272700				
Total Bacillariophyta	**1258730**	**93150**	**6650**	**0**	**0**
Cryptomonas ovata	30050	30050			
Rhodomonas minuta	47370	129600	7360		
Total Cryptophyta	**77420**	**159650**	**7360**	**0**	**0**
TOTAL BIOVOLUME	**1336394**	**280017**	**3162430**	**5495150**	**71442**

Table D19: Wappa Lake 1994 phytoplankton biovolumes (um^3/mL). Blank indicates zero biovolume.

Taxon	3-May	25-May	20-Jun	7-Jul	19-Jul	2-Aug	16-Aug	13-Sep
Aphanizomenon flos-aquae				1829				
A. flos-aquae (heterocytes)				0				
Nodularia spumigena								228
N. spumigena (heterocytes)								0
Total N-fixing Cyanophyta	**0**	**0**	**0**	**1829**	**0**	**0**	**0**	**228**
Chroococcus sp.	1936	1088		4559	33004	8313	3949	
Gomphosphaeria sp.	493		181	6558		1334	912	4941
Merismopedia minima				239			60	
Microcystis aeruginosa		41152	10911	23735	35	6621	56073	32497
Phormidium mucicola						2026		
Pseusanabaena sp.					3561			
Rhabdoderma sp.	3278							
Total other Cyanophyta	**5707**	**42240**	**11092**	**35091**	**36600**	**18294**	**60994**	**37438**
Ankistrodesmus sp.						9		
Ankyra sp.				5602	1178	2182	527	1010
Botryococcus braunii			3180					
Coelastrum sp.	480							
Crucigenia quadrata				3667	443	2084		443
Oocystis borgei	36368	3451	1710	4525	16373	55440	4923	6248
Total Chlorophyta	**36848**	**3451**	**4890**	**13794**	**17994**	**59715**	**5450**	**7701**
Cyclotella sp.	10198					340	3951	3923
Fragilaria crotonensis	4164							1449
Frustulia rhomboides			475					
Gomphonema sp.	2245							
Melosira granulatum	7718							
Navicula sp.	1039			140				
Nitzchia sp.	1303			416	4321	38	927	409
Surirella sp.	10252						5935	14503
Total Bacillariophyta	**36919**	**0**	**475**	**556**	**4321**	**378**	**10813**	**20284**
Cryptomonas sp.	2181		205	35700	2586	8595		18857
Rhodomonas minuta		34		83610	2796	11050		46158
Total Cryptophyta	**2181**	**34**	**205**	**119310**	**5382**	**19645**	**0**	**65015**
Chrysophyte cyst	10544		788	8491	564			
Total Chrysophyta	**10544**	**0**	**788**	**8491**	**564**	**0**	**0**	**0**
TOTAL BIOVOLUME	**92199**	**45725**	**17450**	**179071**	**64861**	**98032**	**77257**	**130666**

Table D20: Whites Lake 1987 phytoplankton biovolumes (um^3/mL). Blank indicates zero biovolume.

Taxon	15-May	11-Jun	15-Jul	13-Aug
Anabaena flos-aquae		32800		
Anabaena sp.		139000		
Aphanizomenon flos-aquae	302000	1400000		
A. flos-aquae (heterocytes)	2220	2370		
Total N-fixing Cyanophyta	**304220**	**1574170**	**0**	**0**
Rhodomonas minuta		11100		66800
Total Cryptophyta	**0**	**11100**	**0**	**66800**
Chrysochromulina parva	16700	12500	12500	
unknown chrysophyte				21800
Total Chrysophyta	**16700**	**12500**	**12500**	**21800**
TOTAL BIOVOLUME	**320920**	**1597770**	**12500**	**88600**

Table D21: Whites Lake 1991 phytoplankton biovolumes (um^3/mL). Blank indicates zero biovolume.

Taxon	15-May	4-Jun	26-Jun	16-Jul	17-Sep
Microcystis aeruginosa	2650		56520	58640	8721
Oscillatoria utermoelii			2870		
Total other Cyanophyta	**2650**	**0**	**59390**	**58640**	**8721**
Surirella ovata		4990	32300	32300	66800
Total Bacilliarophyta	**0**	**4990**	**32300**	**32300**	**66800**
TOTAL BIOVOLUME	**2650**	**4990**	**91690**	**90940**	**75521**

Table D22: Whites Lake 1994 phytoplankton biovolumes (um^3/mL). Blank indicates zero biovolume.

Taxon	3-May	25-May	20-Jun	7-Jul	19-Jul	2-Aug	16-Aug	13-Sep
Anabaena flos-aquae								71
A. flos-aquae (heterocytes)								15
Nodularia spumigena						2345		
N. spumigena (heterocytes)						175		
Total N-fixing Cyanophyta	**0**	**0**	**0**	**0**	**0**	**2520**	**0**	**86**
Gomphosphaeria sp.				352		486		6972
Merismopedia minima	444	1002						
Microcystis flos-aquae			890					
Total other Cyanophyta	**444**	**1002**	**890**	**352**	**0**	**486**	**0**	**6972**
Ankyra sp.		123	3510	90	1766	37	1133	94
Crucigenia quadrata	4490	11704	17396	857	4810	14350	5772	648
Oocystis borgei		4574	82757	4343	6652	2473	28254	
Total Chlorophyta	**4490**	**16401**	**103663**	**5290**	**13228**	**16860**	**35159**	**742**
Amphiphora sp.							391	
Cyclotella sp.		1448	962	628	966	411	4751	250
Frustulia sp.							7211	
Navicula sp.						69	58	
Nitzchia sp.		832	388		2239			23
Total Bacillariophyta	**0**	**2280**	**1350**	**628**	**3205**	**480**	**12411**	**273**
Rhodomonas minuta			1122	15275		957177	949	
Total Cryptophyta	**0**	**0**	**1122**	**15275**	**0**	**957177**	**949**	**0**
TOTAL BIOVOLUME	**4934**	**19683**	**107025**	**21545**	**16433**	**977523**	**48519**	**8073**

Table D23: Vernon Lake 1994 phytoplankton biovolumes (um^3/mL). Blank indicates zero biovolume.

Taxon	2-Jun
Oscillatoria sp.1	33580
Oscillatoria sp.2	308600
Spirulina sp.	13083
Total other Cyanophyta	**321683**
Navicula sp.	9070
Total Bacillariophyta	**9070**
Cryptomonas sp.	1133
Rhodomonas minuta	850
Total Cryptophyta	**1983**
Chrysophyte cyst	150300
Total Chrysophyta	**150300**
TOTAL BIOVOLUME	**483036**

Appendix E:

Data from 1994 bottle bioassay experiments.

Table E1: Bioassay treatments

Experiment	Date water sampled	Lakes	Treatments:
1#	3-May	Br, Cp, Ck, Jp, Mq, Th, Wp, Wh.	Unseeded control, control, Mo (160 ug/L), Fe (850 ug/L) + EDTA (8 mg/L).
2#	25-May	Br, Wp, Wh.	Control, Fe (850 ug/L) + EDTA (8 mg/L), Fe only, EDTA only, Mo (160 ug/L), Mo+Fe+EDTA, trace nutrients*, culture medium spike**, trace metals+EDTA.
3	20-Jun	Br, Cp, Ck, Jp, Mq, Th, Wp, Wh.	Control, Fe (1.3 mg/L) + EDTA (12 mg/L), Fe only, EDTA only, Mo (240 ug/L), Mo+Fe+EDTA, Mo+Fe+EDTA+ trace nutrients*, native zooplankton.
4	19-21 July	Br, Cp, Ck, Jp, Mq, Th, Wp, Wh.	Control, $NH4^+$ (250 ug/L N), NO_3^- (250 ug/L N), NO_3^- + Mo (240 ug/L), Fe (1.3 mg/L) + EDTA (12 mg/L), Mo+Fe+EDTA, HPO_4 (250 ug/L P) Cp and Ck only.
5a	2-Aug	Fg, Pn, Vn.	Control, $NH4^+$ (250 ug/L N), NO_3^- (250 ug/L N), Mo (240 ug/L), NO_3^- + Mo , Fe (1.3 mg/L) + EDTA (12 mg/L), Mo+Fe+EDTA, Fe+EDTA+ trace nutrients*, Mo+Fe+EDTA+ trace metals*.
5b	2-Aug	Br, Jp, Mq, Th, Wp, Wh.	Control, Fe (1.3 mg/L) + EDTA (12 mg/L), NaOH (pH 10.5), H_2SO_4 (pH 7.5).
6	13-Sep	Br, Jp, Mq, Th, Wp, Wh.	Control, native zooplankton, filtered (0.45 um), Fe (1.3 mg/L) + EDTA (12 mg/L), H2SO4 (1/2 alkalinity).
7	13-Sep	Br, Jp, Mq, Th, Wp, Wh.	Control, Fe (1.3 mg/L) + EDTA (12 mg/L), EDTA, H2SO4 (1/4 alkalinity), H2SO4 (1/2 alkalinity), unseeded control.
8	13-Sep	Br, Wp.	Control, filtered (0.45 um), Fe (1.3 mg/L) + EDTA (12 mg/L), Fe (250 g/L) + EDTA (2.4 mg/L), $FeCl_3$ (1.3 mg/L Fe), H2SO4 (1/2 alkalinity), filtered+H2SO4, filtered+Fe+EDTA.

* trace nutrient doses (values are in ug/L) 170 B, 500 Mn, 60 Zn, 18 Cu, 5 Co.

**culture medium includes trace nutrients, iron, EDTA and Mo at 0.2% of dose used in other treatments

#data from these experiments was not used in the study due to problems with (1) addition of unwanted nutrients with cultured "seed" and (2) poor replication due to low cell numbers in the lakewater, which was not seeded

Table E2: Results of bottle bioassay experiment 3. Chlorophyll *a* concentrations are in ug L-1, nine days post inoculation. s.d.= standard deviation *indicates different from control ($P < 0.05$)

	Treatment:					
Lake	Control	Fe/EDTA	Mo	Fe/EDTA/Mo	Fe/EDTA/Mo/Trace	Zooplankton
Birch	70	166	251	127	126	121
s.d.	29	28	148	17	38	130
Camp	40	46	34	45	45	37
s.d.	5	3	5	4	2	2
Cooking	36	*64	*63	*62	*70	49
s.d.	8	11	9	2	12	2
Joseph	449	*1336	494	*1547	*1302	160
s.d.	62	150	65	217	450	62
Miquelon	62	114	140	135	84	59
s.d.	28	18	39	57	5	8
Thomas	214	242	325	201	204	*397
s.d.	15	5	46	37	53	141
Wappa	407	*831	461	*1010	*834	89
s.d.	85	186	140	93	61	45
Whites	278	858	569	448	595	*61
s.d.	35	329	433	111	268	54

Table E3: Results of bottle bioassay experiment 4. Chlorophyll *a* concentrations are in ug L-1, 14 days post inoculation. s.d.= standard deviation *indicates different from control ($P < 0.05$)

	Treatment:							
Lake	Control	NH_4^+	NO_3^-	NO_3^- +Mo	Mo	Fe/EDTA	Fe/EDTA/Mo	Phosphate
Birch	256	512	701	683	511	*1604	*1693	
s.d.	182	179	315	213	272	606	442	
Camp	37	40	42	38	32	39	46	34
s.d.	8	11	5	8	8	10	3	4
Cooking	49	76	80	71	77	72	65	*213
s.d.	8	4	22	23	13	11	13	92
Joseph	453	*1881	998	547	549	*2446	*2092	
s.d.	132	316	397	17	127	446	159	
Miquelon	105	100	71	87	72	121	91	
s.d.	17	14	25	23	35	8	47	
Thomas	1688	1341	1485	1524	1253	*3400	*2749	
s.d.	550	181	257	320	114	182	180	
Wappa	734	961	1044	655	876	*2331	1181	
s.d.	189	294	445	194	508	828	506	
Whites	1209	2118	1986	1059	1016	*3817	*5244	
s.d.	317	142	886	290	286	1015	1427	

Table E4: Results of bottle bioassay experiment 5a. Chlorophyll *a* concentrations are in ug L-1, 14 days post inoculation. s.d.= standard deviation *indicates different from control ($P < 0.05$)

	Treatment:								
Lake	Control	Fe/EDTA	Fe/EDTA/ Mo	Mo	NO_3^- +Mo	NO_3^-	NH_4^+	Trace/Fe/ EDTA	Trace/Fe/ EDTA/Mo
Fluevog	548	*2723	*2457	659	1079	1373	*2029	*2391	*2519
s.d.	204	398	626	24	112	264	345	654	285
Peninsula	577	*5654	*3855	720	1144	1069	1343	*5171	*4297
s.d.	186	1243	856	362	506	204	104	480	1423
Vernon	43	96	118	50	84	112	108	*178	*227
s.d.	7	11	21	11	22	13	26	2	78

Table E5: Results of bottle bioassay experiment 5b. Chlorophyll *a* concentrations are in ug L-1, 14 days post inoculation. s.d.= standard deviation *indicates different from control ($P < 0.05$)

Lake	Treatment: Control	Fe/EDTA	NaOH (pH10.5)	H_2SO_4 (pH 7.5)
Birch	411	*3097	231	*1754
s.d.	62	682	145	303
Joseph	1019	*2359	1079	1228
s.d.	231	603	31	172
Miquelon	82	57	62	91
s.d.	11	19	7	20
Thomas	547	*2003	461	966
s.d.	139	616	162	182
Wappa	1219	*1922	*441	*1229
s.d.	90	231	23	221
Whites	1428	*3159	536	*3011
s.d.	595	757	176	206

Table E6: Results of bottle bioassay experiment 6. Chlorophyll *a* concentrations are in ug L-1, 14 days post inoculation. s.d.= standard deviation *indicates different from control ($P < 0.05$)

	Treatment:				
Lake	Control	Zooplankton	0.45-um filtered	Fe/EDTA	H_2SO_4 (50% of alkalinity)
Birch	741	803	1109	*2507	*1742
s.d.	306	591	138	397	331
Joseph	743	857	328	*2632	*3792
s.d.	187	166	315	856	514
Miquelon	90	78	83	84	147
s.d.	31	15	16	13	36
Thomas	941	541	1070	*4287	
s.d.	297	98	225	1065	
Wappa	2555	2318	812	5687	2571
s.d.	275	257	264	2637	222
Whites	1008	584	436	*5872	1025
s.d.	227	437	115	744	731

Problems with alkalinity determination led to overacidification of Thomas Lake bioassay

Table E7: Results of bottle bioassay experiment 7. Chlorophyll *a* concentrations are in ug L-1, 14 days post inoculation. s.d.= standard deviation *indicates different from control ($P < 0.05$)

	Treatment:					
Lake	Control	Fe/EDTA	EDTA	H_2SO_4 (25% of alkalinity)	H_2SO_4 (50% of alkalinity)	0.45-um filtered
Birch	1834	*6382	1266	*7237	*6514	*41
s.d.	607	588	586	2330	364	10
Joseph	1134	*6337	1066	1857	*3816	*10
s.d.	360	735	224	557	3443	5
Miquelon	83	89	68	139	130	
s.d.	38	5	8	38	3	
Thomas	1152	*7575	1212	*2699	1829	355
s.d.	82	984	685	219	632	63
Wappa	469	*12140	1263	*6829		
s.d.	305	2445	651	2074		
Whites	2123	*10000	1275	*7366	*11089	*85
s.d.	1244	421	410	894	154	62

Problems with alkalinity determination led to overacidification of Wappa Lake bioassay. Filtration treatment not run for Miquelon and Wappa lakewater due to space constraints.

Table E8: Results of bottle bioassay experiment 8. Chlorophyll *a* concentrations are in ug L-1, 35 days post inoculation. s.d.= standard deviation *indicates different from control ($P < 0.05$)

	Treatment:							
Lake	Control	0.45-um filtered	Fe/EDTA	Fe/EDTA (low)	$FeCl_3$	H_2SO_4 (50% of alkalinity)	filtered+ H_2SO_4 (50% of	0.45-um filtered + Fe/EDTA
Birch	4396	3182	*18660	*7134	*22890	*20800	9720	*22180
s.d.	1181	2730	1070	1270	2890	3710	2440	283
Wappa	918	284	*6170	4749	*7125	5376	2752	*13412
s.d.	63	146	2800	962	925	2230	4660	460